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Volume LII 1965 Nos. 1-4

Annals
of the
Missouri Botanical Garden

Dates of Publication for Volume LII

No. 1, pp. 1-98, March 31, 1965

No. 2, pp. 99-222, July 27, 1965

No. 3, pp. 223-486, October 15, 1965

No. 4, pp. 487-604, January 5, 1966

PUBLISHED QUARTERLY BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN
AND WASHINGTON UNIVERSITY PRESS
ST. LOUIS, MISSOURI

MISSOURI BOTANICAL
GARDEN LIBRARY

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ERRATA IN VOLUME LII, NO. 1

Page 1. For author of *Lonchocarpus* read F. J. Hermann.

Page 52, line 34. For '*Oleiocarpus*' read '*Oleiocarpon*.'

Volume LII February, 1965 No. 1

Annals
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PUBLISHED QUARTERLY BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN
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ST. LOUIS, MISSOURI

Annals

of the

Missouri Botanical Garden

A quarterly journal containing scientific contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

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Information

THE ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Beginning with Volume 45, 1958:

Subscription Price	$15.00 per volume
Single Numbers	4.00 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Beginning June 1, 1962 the Stechert-Hafner Service Agency, Inc., 31 East 10th St., New York 3, N. Y., became sole agent for the ANNALS OF THE MISSOURI BOTANICAL GARDEN. The Agency handles all subscriptions, all claims beginning with volume 50 (1963) and all requests for back issues. Out-of-print numbers will be reprinted as may be required.

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FLORA OF PANAMA

BY

Robert E. Woodson, Jr.

AND

Robert W. Schery
and collaborators

PART V

Fascicle 4

Family 83. LEGUMINOSAE (in part)

PART VI

Family 92. MELIACEAE

Family 104. HIPPOCRATEACEAE

Annals

of the

Missouri Botanical Garden

Vol. LII FEBRUARY, 1965 No. 1

Annals
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Vol. LII | FEBRUARY, 1965 | No. 1

FLORA OF PANAMA[1]

Part V, Fascicle 4

Family 83. LEGUMINOSAE[2]

Subfamily PAPILIONOIDEAE (in part)[3]

By John D. Dwyer[4]

Lonchocarpus By F. I. Hermann

Trees, shrubs or herbs, occasionally armed. *Leaves* often alternate, pari- or imparipinnate, frequently 3-foliolate, rarely 1-foliolate; stipules usually present; stipelles mostly present. *Inflorescences* usually racemose or paniculate, often axillary. *Flowers* papilionaceous, rarely actinomorphic; hypanthium more or less campanulate, the teeth 5, the carinal tooth often the longest; petals 5, disposed as an upper vexillum or standard, two alae or wing petals, and 2 carinal petals coherent apically, occasionally united in part with the wing petals and enclosing the androecium and the gynoecium, occasionally rostrate or coiled at the apex; stamens 10, rarely 9 or less, occasionally free, usually monadelphous or diadelphous, the free filaments equal or often alternating long and short, the anthers monomorphic or dimorphic; ovary 1-carpellate, often surrounded by a glandular disk, 1- to several-ovulate, the stigma capitate or lateral, often enlarged, occasionally bearded. *Fruits* mostly dehiscing along 2 sutures, often pluri-loculate by the development of septa, occasionally indehiscent and samaroid, drupaceous or lomentaceous; seeds 1-several, often arillate, exalbuminous, the radicle of the embryo curved.

Of the subfamilies of *Leguminosae,* the *Papilionoideae,* whether regarded on

[1] The Flora of Panama by Robert E. Woodson, Jr. and Robert W. Schery and Collaborators should be cited as: Ann. Missouri Bot. Gard., with volume number, pagination and date of the Annals.

[2] Continued from Ann. Missouri Bot. Gard. **38:** 94. 1951 (Flora of Panama **5**(3): 394).

[3] Assisted by National Science Foundation Grants No. G-7144 (Principal Investigator, R. E. Woodson, Jr.) & No. GB-170 (Principal Investigator, H. C. Cutler).

[4] I wish to acknowledge the assistance received from Dr. A. Robyns in preparing the manuscript.

Ann. Missouri Bot. Gard. **52:** 1-54. No. 1. 1965.

a world-wide basis or locally in Panama, contains the greatest number of genera and species and the largest representation of plants economically important, as food, drugs, timber or dyes.

The following publications were found helpful in the preparation of this work:

Amshoff, G. J. H., On South American *Papilionaceae*. Med. Bot. Mus. Herb. Rijksuniv. Utrecht **52:** 1-71, *fig. 1-4.* 1939.

Amshoff, G. J. H., *Papilionaceae* in Pulle, Flora of Suriname **2**(2): 1-257. 1939.

Auctores, *Papilionaceae* in Flore du Congo Belge et du Ruanda-Urundi (Publ. I.N.É.A.C.), Spermatophytes **4**. 1953, **5** & **6**. 1954.

Baillon, H., Légumineuses in Baillon, Histoire des Plantes **2:** 21-384, *fig. 15-157.* 1870.

Bentham, G., *Papilionaceae* in Martius, Flora Brasiliensis **15**(1): 1-216, *tab. 1-56.* 1859, 217-350, *tab. 57-127.* 1862.

Burkart, A., Las Leguminosas Argentinas Silvestres y Cultivadas, 1943.

De Candolle, A. P. Mémoires sur la Famille des Légumineuses. 1825.

De Candolle, A. P., *Leguminosae* in DC., Prodr. **2:** 93-524. 1825.

Ducke, A., As Leguminosas da Amazonia Brasileira (Notas sôbre Flora Neotrópica—II). Bol. Técn. Inst. Agron. Norte (Belém) **18:** 3-248. 1949.

Macbride, J. F., *Mimoseae* in Macbride, Flora of Peru. Field Mus. Nat. Hist., Bot. Ser. **13**(3): 4-113. 1943.

Pellegrin, F., Les Légumineuses du Gabon. Mém. Inst. Étud. Centrafr. Brazzaville **1:** 1-248. *pl. 1-8.* 1949.

Perkins, J., The *Leguminosae* of Porto Rico. Contr. U. S. Nat. Herb. **10:** 133-220. 1907.

Pittier, H., Arboles y Arbustos del Orden de Las Leguminosas. III. *Papilionaceas.* Bol. Min. R.R.E.E. **4-7:** 149-229. 1928.

Standley, P. C., Flora of the Panama Canal Zone. Contr. U. S. Nat. Herb. **27:** I-X, 1-416, *fig. 1-7, pl. 1-66.* 1928.

Standley, P. C., The Flora of Barro Colorado Island, Panama. Contr. Arnold Arb. **5:** 1-17, *pl. 1-21, map.* 1933.

Taubert, P., *Leguminosae* in Engler et Prantl, Nat. Pflanzenfam. **3**(3): 70-288, *fig. 38-136.* 1891-1894.

The complexity of the legumes has discouraged many taxonomists and they are often set aside in favor of other families. While the numbers of species in certain genera of the *Papilionaceae* (e.g. *Astragalus, Lupinus, Rhynchosia, Phaseolus*) may account in part for this attitude, equally disconcerting is the vagueness of generic lines in many complexes: *Dussia-Bowditchia-Diplotropis,* or *Phaseolus-Vigna-Pachyrrhizus,* or *Coumarouna-Dipteryx-Pterodon.*

One of the most discouraging features of studies such as the present, which is based primarily on herbarium materials, is the absence of fruiting specimens. The fruits of many genera are so drab and resemble each other so much in morphology and in texture that collectors tend to by-pass them in the field in favor of flowering material. I estimate that less than 10% of all tropical American collections include mature fruit. In many genera it is imperative to have both flowers and fruits

for critical identification, as in *Mucuna*, and in some species of *Machaerium*. With fruiting collections thus limited, the seed collections in herbaria are obviously poor. This is especially true in the tribe *Dalbergieae* whose fruits are indehiscent and are easily destroyed in the attempt to dissect the seeds.

KEY TO TRIBES

a. Stamens monadelphous or diadelphous.
  b. Trees, tall shrubs or woody lianas; leaves pinnate (rarely 1-foliolate); calyx-teeth much reduced or absent; fruit indehiscent, often winged or drupaceous .... 1. DALBERGIEAE
  bb. Herbs, herbaceous or woody vines or shrubs; leaves usually 3-foliolate; calyx-teeth mostly conspicuous; fruits mostly dehiscent or rarely indehiscent.
    c. Herbs, usually twining; flowers more than 1 cm. long, rarely smaller but then, with glandular-papillate leaves .... 2. PHASEOLEAE
    cc. Shrubs, or erect or sprawling herbs; flowers mostly small but the leaves not glandular-papillate (except *Dalea*).
      d. Fruits not articulate.
        e. Leaves with more than 3 leaflets .... 3. GALEGEAE
        ee. Leaves 1- to 3-foliolate (except *Lupinus*).
          f. Leaves pinnately 3-foliolate, the margins of the leaflets usually denticulate; anthers invariably monomorphic .... 4. TRIFOLIEAE
          ff. Leaves 1-foliolate or digitately 3- to 16-foliolate, the margins of the leaflets usually entire; anthers often dimorphic .... 5. GENISTEAE
      dd. Fruits articulate, or if not, hypogeal .... 6. HEDYSAREAE
aa. Stamens free .... 7. SOPHOREAE

Tribe 1. DALBERGIEAE

Taxonomically the fruits of the *Dalbergieae* are of paramount importance. Few-seeded, indehiscent, and samaroid or drupaceous, they provide excellent delimiting characters, principally at the generic level. Genera of the tribe are usually easy to identify when mature fruit is present. On the other hand, the wide divergence of opinion concerning the definition of generic lines on a world-wide basis stems principally from the matter of interpreting the morphological variation of the fruit. Bentham in his monograph of the *Dalbergieae* (cf. list below) has warned about the need of understanding the fundamental structural plan of the fruit before segregating a genus like *Drepanocarpus* from *Machaerium*.

The following are publications found useful in preparing the manuscript of the *Dalbergieae* of Panama.

Bentham, G. Synopsis of the *Dalbergieae*, a Tribe of *Leguminosae*. Jour. Proc. Linn. Soc., Bot. **4** (Suppl.): 1-134. 1860.

Ducke, A. Revision of the Species of the Genus *Coumarouna* Aubl. or *Dipteryx* Schreb. Trop. Woods **61:** 1-10. 1940.

Johnston, I. M. The Botany of San José Island (Gulf of Panama). Sargentia **8:** I-II, 1-306, 2 fig., 17 pl. 1949.

Pittier, H. On the Species of *Dalbergia* of Mexico & Central America. Jour. Wash. Acad. Sci. **12:** 54-64. 1922.

KEY TO GENERA

a. Fruits membranous, papyraceous or coriaceous, never drupaceous.
 b. Staminal tube cleft along the entire length; fruits with a flat wing, the seed distal or basal (except when wing much reduced, *Pterocarpus*).
  c. Leaves alternate.
   d. Anthers basifixed, dehiscing by 2 horizontal slits; pistil usually glabrous, occasionally moderately pubescent .... 1. DALBERGIA
   dd. Anthers dorsifixed (except some spp. of *Machaerium*) dehiscing by 2 longitudinal slits; pistil usually densely hairy.
    e. Fruits not orbicular, the seminiferous area basal or apical.
     f. Calyx turbinate at the base; pericarp glabrous, the seed apical .... 2. PLATYPODIUM
     ff. Calyx obtuse at the base; pericarp covered in whole or in part with few to many hairs or spines, the seed basal.
      g. Leaves not resinous-lepidote beneath; fruits 3-12 cm. long, the wing lacking a stylar spine.
       h. Fruits 3-8 (-10) cm. long, the wing at least 4 times as long as wide .... 3. MACHAERIUM
       hh. Fruits about 12 cm. long, the wing 3 times as long as wide .... 4. PARAMACHAERIUM
      gg. Leaflets resinous-lepidote beneath; fruits 12-20 cm. long, the wing with an obvious stylar spine .... 5. CENTROLOBIUM
    ee. Fruits orbicular, the seminiferous area median, the wing rudimentary .... 6. PTEROCARPUS
  cc. Leaves opposite .... 7. PLATYMISCIUM
 bb. Staminal tube open only basally; fruits 4-angular, flat or terete, the seed median.
  c. Fruits 4-angular; ovary sessile .... 8. PISCIDIA
  cc. Fruits flat or terete; ovary usually stipitate.
   d. Vexillum not auriculate; fruits terete .... 9. MUELLERA
   dd. Vexillum usually auriculate; fruits flat .... 10. LONCHOCARPUS
aa. Fruits drupaceous.
 b. Anthers dehiscing by 2 terminal pores; calyx spathaceous .... 11. FISSICALYX
 bb. Anthers dehiscing by longitudinal slits; calyx not spathaceous.
  c. Rachis of the leaves terete; hypanthium truncate at the base; calyx-lobes scarcely evident, not glandular-punctate; ovary sparsely hairy (rarely glabrous); fruit not oleaginous .... 12. GEOFFROEA
  cc. Rachis of the leaves alate; hypanthium rounded at the base; calyx-lobes glandular-punctate; ovary glabrous; fruits oleaginous .... 13. OLEIOCARPON

1. DALBERGIA L. f.

Dalbergia L. f., Suppl. Pl. Syst. Veg. 52. 1781, nom. gen. conserv.

Amerimnon P. Br., Civ. Nat. Hist. Jam. 288. 1756.
Ecastaphyllum P. Br., loc. cit. 299. 1756.
Acouroa Aubl., Hist. Pl. Gui. Fr. 753. 1775.

Trees or shrubs. *Leaves* imparipinnate, the leaflets usually alternate, 3 to several, rarely 1; stipules ovate to subulate, small. *Inflorescences* paniculate (occasionally racemose), terminal or axillary. *Flowers* small, on short pedicels; bracts and bracteoles soon deciduous; hypanthium subgibbous, campanulate, the teeth 5; petals subequal, clawed, the carinal petals coherent along the lower margin; stamens 10, monadelphous or disposed in 2 fascicles of 5, the anthers minute, basifixed, dehiscing by 2 horizontal slits; ovary obviously stipitate, the style subulate, the stigma capitate or indeterminate. *Fruits* stipitate, oblong to rotund, occasionally

constricted medially, wingless or with the wing surrounding the seminiferous area, lightly reticulate, the margin not thickened, the seeds solitary or rarely 2, flat.

About 200 species in the tropics of the Old World and the New World.

a. Leaves several-foliolate; inflorescences patulous.
  b. Carinal tooth of hypanthium not equal to or exceeding the fused portion in length; blade of vexillum subcuneate.
    c. Hypanthium obviously carnose; ovary glabrous, fruit at maturity flat .... 1. D. CUSCATLANICA
    cc. Hypanthium petaloid to scarcely carnose; ovary rarely glabrous; fruit at maturity nummiform, at maturity turgid .... 2. D. MONETARIA
  bb. Carinal tooth of hypanthium equal to or exceeding the fused portion in length; blade of vexillum subreniform; pistil glabrous .... 3. D. RETUSA
aa. Leaves 1-foliolate; inflorescences compressed.
  b. Leaflets ovate-oblong, oblong or oblong-rotund, rarely ovate, 2-8 cm. wide; flowers crowded; style about 2.5 mm. long .... 4. D. ECASTOPHYLLA
  bb. Leaflets ovate, up to 5 cm. wide; flowers patulous; style up to 1.7 mm. long .... 5. D. BROWNEI

1. DALBERGIA CUSCATLANICA (Standley), Standley, Field Mus. Nat. Hist., Bot. Ser. **4**: 215. 1929.

Amerimnon cuscatlanicum Standley, Jour. Wash. Acad. Sci. **13**: 442. 1926.
Dalbergia pacifica Standley & Steyerm., Field Mus. Nat. Hist., Bot. Ser. **22**: 236. 1940.

Tree, small. *Leaves* up to 22 cm. long; leaflets 12-14, oblong or lanceolate-oblong, 6-12 cm. long, 2.5-5 cm. wide, deltoid, short-acuminate or obtuse at the apex, membranous, concolor, smooth, reticulate, glabrous above, pilulose or sericeous beneath, the margin revolute, the secondary veins arcuate; stipules narrowly rectangular, about 1.5 cm. long, falcate at the apex. *Panicles* up to 5 cm. long, the branches stiff and thick, or slender and deflexed, up to 2 cm. long, the pedicels about 3 mm. long, slender, puberulent. *Flowers* with the hypanthium up to 5 mm. long, very carnose, drying black, the teeth subequal, oblong to rotund, 1-2 mm. long; vexillum obovate-oblong, about 15 mm. long, about 10 mm. wide, obtuse at the base, the claw about 0.5 mm. long, glabrous; wing petals narrowly falcate-oblong, up to 14 mm. long, up to 4.5 mm. wide, the basal auricle suborbicular, about 1 mm. long, glabrous, the claw about 4.5 mm. long; carinal petals subreniform, equal to the wing petals, the basal auricle about 1.5 mm. long, the claw about 4 mm. long; stamens monadelphous or diadelphous, glabrous, the sheath and filaments subequal in length, the anthers about 0.3 mm. long; ovary stipitate for 4 mm., glabrous, 4-ovulate, the style about 4 mm. long. *Fruits* with the stipe 1-2 cm. long, narrowly oblong, up to 12 cm. long, about 2 cm. wide, glabrous, occasionally glaucous, lustrous.

Guatemala, Costa Rica and Panama.

PANAMA: Bejuco, *Allen 2457*. PROVINCE UNKNOWN: *R. S. Williams s. n.*

The inflorescences of *D. cuscatlanica* are much more compressed than those of *D. retusa*. The rachis of its inflorescence is more stout and the fruits are obviously more plano-compressed than those of *D. monetaria*. The flowers are described as white.

2. Dalbergia monetaria L. f., Suppl. Pl. Syst. Veg. 317. 1781.

Securidaca volubilis L., Sp. Pl. 707. 1753, pro parte.
Ecastaphyllum monetaria (L. f.) Pers., Syn. Pl. **2:** 277. 1807.
Ecastophyllum benthamianum Miq., Linnaea **18:** 575. 1844.
Dalbergia brownei Schinz, Bull. Herb. Boiss. **6:** 731. 1898, non Jacq. 1756.
Dalbergia volubilis (L.) Urban, Repert. Sp. Nov. **16:** 136. 1919.

Shrub or small tree. *Leaves* with 3-5 leaflets, these elliptic, 4.5-15 cm. long, 2-7 cm. wide, the acumen up to 1.8 cm. long, the margins slightly callose, the blade thinly coriaceous, drying brown; petioles 1-2 cm. long, slender; rachises 3-10 cm. long, wiry, puberulent. *Inflorescences* axillary, the rachises about 2 cm. long, slender, puberulent. *Flowers* with the hypanthium gibbous-campanulate, about 1.7 mm. long, glabrous or puberulent, the teeth subequal, minute, about 0.6 mm. long; vexillum oblong-rotund, up to 7.5 mm. long, up to 3.2 mm. wide, the claw equal to the blade, glabrous; wing petals narrowly oblong, up to 5 mm. long, truncate, oblique at the base, the claw about 1.8 mm. long; carinal petals narrowly falcate-oblong, about 5 mm. long, obtuse, glabrous; stamens in 2 fascicles of 5, the sheath slightly longer than the filaments, glabrous, the anthers about 0.2 mm. long; ovary slender-stipitate for about 3 mm., puberulent marginally, the erect style about 1.5 mm. long, puberulent at the apex only. *Fruits* with the stipe about 0.5 cm. long, nummiform (when young), rotund at maturity, about 3.5 cm. long, lustrous, glabrous; seeds somewhat flat, up to 1.5 cm. long.

Known from Mexico, Central America, and northern South America.

colón: Río Sirrí, Trinidad Basin, *Pittier 4029.*

Oort, in a critical study of the genus *Securidaca* (*Polygalaceae*) in Surinam (Med. Bot. Mus. Herb. Rijksuniv. Utrecht **36:** 677-685. 1939), discusses (pp. 678-679) the fact that the Linnaean type of *Securidaca* is *S. volubilis* L.; the type material consists of three sheets, one of which, according to Oort, contains a fragment of the legume *Nissolia.* Amshoff in Pulle's Flora of Suriname (**2**(2): 120. 1939) presumably regards the fragment of the legume as belonging to the genus *Dalbergia*, as she cites *S. volubilis* L. in the synonomy of *D. monetaria* L. f.

Pittier (in his key to the *Dalbergia* of Mexico, Jour. Wash. Acad. Sci. **12:** 55-56. 1922) describes *D. monetaria* as having 9 stamens. My floral dissections reveal a constant number of 10. *Dalbergia* appears to be exceptional in the *Papilionoideae* in having more species than any other genus with a constant number of 9 stamens (e.g. *D. sisso, D. melanocardium, D. glomerata*).

3. Dalbergia retusa Hemsl., Diag. Pl. Nov. Mex. Centr.-Am. 8. 1878, non Baillon. 1884.

Dalbergia lineata Pittier, Jour. Wash. Acad. Sci. **12:** 63. 1922.
Amerimnon lineatum (Pittier) Standley, Jour. Wash. Acad. Sci. **13:** 442. 1923.

Tree. Leaves with 7-15 leaflets, these inequilaterally oblong or ovate-oblong, 2.5-12 cm. long, 2-7 cm. wide, shortly acuminate or obtuse, chartaceous to coriaceous,

lustrous, reticulate, glabrous to puberulent, the costa plane above, the margins revolute; stipules ovate, up to 0.7 cm. long; petioles 4-5 cm. long. *Panicles* axillary or terminal, the rachises 4-18 cm. long, puberulent, the branches few; bracts and bracteoles soon deciduous, the latter oblong, about 1 mm. long. *Flowers* with the hypanthium cupuliform, about 5 mm. long, glabrous, the teeth deltoid, 1.7-3.1 mm. long, the longer carinal tooth puberulent on the outside; floral parts glabrous; vexillum cucullate-subrotund, up to 13.5 mm. long, cordate or subreniform basally, the claw 3-4 mm. long; wing petals oblong, about 13 mm. long, about 5 mm. wide, venose; carinal petals subreniform, up to 12 mm. long; stamens monadelphous or diadelphous, the sheath 3.5-7 mm. long, the free filaments curving and upright, subulate, up to 5 mm. long, the anthers about 0.3 mm. long; ovary stipitate for about 4 mm., 4-ovulate, the style curved, 4-5.5 mm. long. *Fruits* with the stipe 3-10 mm. long, narrowly oblong, 6-13 cm. long, 1.5-2.2 cm. wide, cuneate, obtuse or subtruncate, cuneate basally, glaucous, 1 to 2 (-3)-seeded; seeds flat, oblong.

Known from Mexico, Nicaragua, Costa Rica, and Panama.

CANAL ZONE: Madden Dam, *Baker 496;* Ancón, *Harvey 5183;* across Canal from Balboa, *Mell 2;* Experimental Gardens, *Skeete 551;* Cerro Gordo, Culebra, *Standley 25962.* COCLÉ: Penonomé, *R. S. Williams 425.* DARIEN: La Palma, *Pittier 6606.* PANAMA: Sabanas, *Bro. Paul 303;* Chagres River, Alhajuela, *Pittier 3531;* Arraiján & Chorrera, *Allen 4316;* Matías Hernández & Juan Díaz, *Standley 31961;* without locality, *Hayes 642.*

The leaflets of *D. retusa* are quite variable in size, shape and texture with those of the Costa Rican collections being thicker, more obtuse or retuse at the apex, and often more oblique at the base. Presumably additional collections in Panama will have oblong-rotund leaflets like the Costa Rican *Standley & Valerio 44124.* Noteworthy is *Pittier 6606,* cited above, with fruits measuring up to 13 cm. in length and with the proximal third of the wing obviously narrower.

The wood of *D. retusa* is the famous *rosewood* or *cocobolo.* Record and Hess (Timbers of the New World 255. 1943) state: "Insofar as the structure, properties, and utility of the timber is concerned cocobolo from Panama to Mexico may be considered as one species, *D. retusa.*" Record and Garratt, in discussing the economic importance of *cocobolo* (Yale Univ., School For., Bull. **8:** 1-42, 7 *pl.* 1923), stress the exploitation of *D. retusa* in Panama.

D. retusa Baillon (Bull. Soc. Linn. Paris **1:** 436. 1884) was applied to a collection from Madagascar and is an earlier homonym of *D. retusa* Hemsl.

4. DALBERGIA ECASTAPHYLLA (L.) Taub. in Engl. & Prantl, Nat. Pflanzenfam. **3**(3): 335. 1894.—Fig. 133.

Hedysarum ecastaphyllum L., Syst. Nat. ed. 10, 1169. 1759.
Ecastaphyllum brownei Pers., Syn. Pl. **2:** 277. 1807, non Jacq. 1756.
Ecastophyllum ecastophyllum (L.) Britton, Mem. Brooklyn Bot. Gard. **1:** 55. 1918.
Amerimnon ecastophyllum (L.) Standley, Jour. Wash. Acad. Sci. **15:** 459. 1925.

Shrub or small tree. *Leaves* 1-foliolate, the leaflets ovate or oblong, or oblong-rotund, 2.5-14 cm. long, 2-8 cm. wide, obtuse or obcordate at the apex, coriaceous, lustrous, puberulent, the costa often plane below, the margins somewhat irregular,

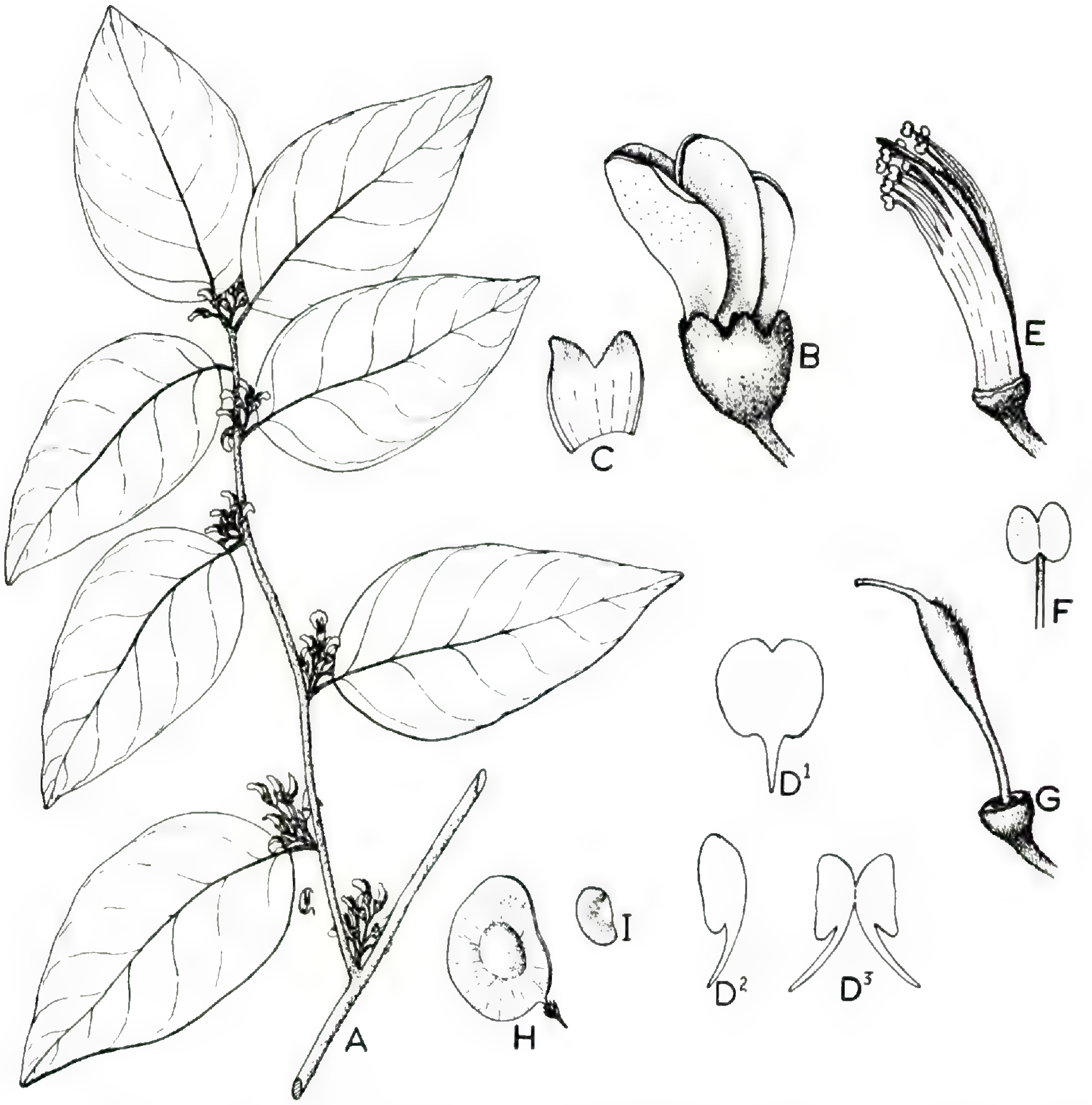

Figure 133. Dalbergia ecastophylla (L.) Taub.: A, flowering branch (× 1); B, flower (× 8); C, calyx in part (× 8); D, petals (× 5), D[1], vexillum, D[2], wing, D[3], carina; E, androecium (× 10); F, anther and filament (× 50); G, gynoecium and receptacle (× 10); H, fruit and persistent calyx (× 1); I, seed (× 1). After *von Wedel 447* (MO).

moderately revolute; petioles and petiolules 0.3-1 cm. long, slender; stipules ovate or widely subulate, up to 0.2 cm. long. *Inflorescences* congested in the axils, the slender rachises up to 2 cm. long, densely ferruginous-puberulent, the pedicels 1-3 mm. long; bracts rotund, ovate or reniform, 1-1.5 mm. long. *Flowers* with the hypanthium about 4 mm. long, aurous-puberulent, the teeth submammiform to deltoid, up to 1 mm. long, the carinal tooth usually narrower and longer; petals glabrous; vexillum suborbicular, up to 9 mm. long, the claw about 3 mm. long; wing petals oblong, up to 9.5 mm. long, obtuse, the claw about 3.3 mm. long; carinal petals gibbous, oblong-rotund, 6-7 mm. long, about 3 mm. wide; stamens monadelphous or in 2 fascicles of 5, the sheath 3-5 mm. long, the filaments up to 2 mm. long; ovary stipitate for 2-2.5 mm., moderately aurous-puberulent, the style about 1.7 mm. long. *Fruits* with the stipe about 0.3 cm. long, oblong-rotund to

narrowly oblong, 1.2-3.5 cm. long, up to 2.3 cm. wide, obtuse at the apex, obtuse to cuneate at the base, rarely constricted medially; seeds flat, oblong, up to 1.5 cm. long.

Tropical Florida, West Indies, Mexico, Central America, south to Rio de Janeiro, Brazil.

BOCAS DEL TORO: Isla Colón, *von Wedel 518;* Chiriquí Lagoon, *Hart 182, von Wedel 898, 1138, 1332, 2059, 2104, 2810;* without locality, *von Wedel 447, 1676.*

5. DALBERGIA BROWNEI (Jacq.) Urban, Symb. Ant. **4**: 295. 1905.

Amerimnon brownii Jacq., Enum. Syst. Pl. Carib. 27. 1760.
Dalbergia amerimnum Benth., Jour. Proc. Linn. Soc. Bot. **4** (Suppl.): 36. 1860.

Shrub or tree, often densely branched. *Leaves* 1-foliolate, the leaflets ovate to ovate-oblong, up to 9.5 cm. long, up to 5 cm. wide, obtuse or tapering gradually, the acumen vague or obvious, variable at the base, coriaceous, lustrous, often subbulate above, puberulent, the costa subplane or subimmersed above; petioles 0.3-1 cm. long; stipules ovate to widely subulate, up to 0.2 cm. long. *Inflorescences* cymose-paniculate, the rachises shorter than the leaves; pedicels about 1.5 mm. long, puberulent; bracts ovate or reniform-ovate, up to 1.5 mm. long; bracteoles oval to oblong-lanceolate, 0.6-1 mm. long; *Flowers* with the hypanthium about 4 mm. long, the teeth minute, the carinal tooth about twice the length of the others, up to 1.8 mm. long; vexillum narrowly oblong to rectangular, up to 9 mm. long; wing petals narrowly oblong, up to 9.5 mm. long, obtuse, the claw about 3.5 mm. long; stamens monadelphous, the filaments and the sheath subequal in length; ovary stipitate for 2-4 mm. glabrous to minutely puberulent, the style about 1.5 mm. long. *Fruits* stipitate for about 0.3 cm. long, oblong-rotund to narrowly oblong, 1.2-3.5 cm. long, up to 2.5 cm. wide, obtuse at the apex, obtuse to cuneate basally, flat, rarely constricted medially, smooth, lustrous; seeds flat, oblong or oblong-rectangular, up to 1.5 cm. long.

Florida, West Indies, Mexico, Central America, and throughout South America.

BOCAS DEL TORO: Chiriquí Lagoon: *von Wedel 2374, 2436, 2547;* Isla Colón, *von Wedel 502.* CANAL ZONE: Victoria Fill near Miraflores Lake, *Allen 1758;* Gatun Station, *Hayes 1012;* Fort Randolph, *Maxon & Harvey 6503; Standley 28610;* France Field, *Standley 30304;* Fort Sherman, *Johnston 1765; Standley 30931;* Balboa, *Standley 32148.* COLÓN: Fato & Playa de Damas, *Pittier 38341.* PANAMA: San José Island, *Erlanson 8, Johnston 516;* Paitilla, *Standley 26259, 30790;* Taboga Island, *Standley 27956.* VERAGUAS: Isla de Coiba, *Dwyer 1667.*

2. PLATYPODIUM Vogel

PLATYPODIUM Vogel, Linnaea **11**: 420. 1837.

Callisema Benth. ex Steud., Nom. Bot. ed. 2, **1**: 258. 1840.

Trees small, unarmed. *Leaves* imparipinnate, the leaflets alternate or subopposite, oblong, the secondary veins numerous; stipules minute, caducous. *Racemes* lax, disposed in the upper axils; bracts and bracteoles small, deciduous. *Flowers*

with the calyx turbinate, the 5 teeth bilabiately disposed, the upper teeth coherent almost to the apex; vexillum large, orbicular; wing and carinal petals oblong or obovate, the carinal petals shorter; stamens 10, with usually the vexillar and carinal filaments relatively free, the remaining disposed in 2 fascicles of 4, the anthers versatile; ovary with the stipe obviously elongate and surrounded by a glandular disk, the style glabrous, the stigma small, terminal. *Fruits* indehiscent, samaroid, glabrous, the seminiferous area distal, subligneous, the wing (expanded stipe) oblong, coriaceous, venose; seeds 1-2, oblong, reniform, the rostellum hard, conical.

A small genus known from Panama, Venezuela, Brazil, Colombia, and Peru.

1. Platypodium elegans Vogel, Linnaea **11:** 420. 1837.—Fig. 134.

Playtypodium viride Vogel, loc. cit. 422. 1837.
Platypodium elegans var. *major* Benth. in Mart., Fl. Bras. **15**(1): 262. 1862.
Platypodium maxonianum Pittier, Contr. U. S. Nat. Herb. **18:** 234. 1917.

Tree, small, the trunk with sinuate, convolute ridges. *Leaves* up to 20 cm. long, the leaflets 10-20, oblong, up to 7.5 cm. long, 1.5-3 cm. wide, the principal secondary veins about 25, arcuate, the margins thickened, the blade thinly coriaceous, puberulent below, lustrous above, the rachises about 7.5 cm. long; petioles up to 1.5 cm. long, puberulent. *Flowers* with pedicels about 4 mm. long; hypanthium campanulate, about 8.5 mm. long, pilulose within, the upper pair of teeth deltoid, about 3.3 mm. long, the lower 3 oblong to rotund, about 2 mm. long; vexillum obovate-rotund, about 18 mm. long, narrowly cuneate at the base; wing petals not seen; carinal petals reniform, up to 12.5 mm. long, the auricles obtuse, the claw obviously eccentric; stamens diadelphous, the sheeth more than twice the length of the filaments, the anthers about 0.6 mm. long; ovary stipitate for about 5 mm., sparsely villose. *Fruits* with the stipe obviously long-winged and cuneate basally, the pedicels about 1 cm. long, the seminiferous area distal, obliquely oblong, up to 3 cm. wide, turgid, the veins prominulous, dense, oblique.

Panama and northern South America.

canal zone: Barro Colorado Island, *Aviles 33, Bangham 388, Carpenter 39, 54, Dwyer 1448, Kenoyer 389, 596, Shattuck 1124, Standley 31299, Wetmore & Abbe 183, Woodworth & Vestal 550.* chiriquí: Comarca del Barú, *Stern & Chambers 125;* San Felix, *Pittier 5229.* darien: El Real, *Stern, Chambers, Dwyer & Ebinger 191.*

The fruits with a winged stipe and a turgid distal seminiferous area bear a fancied resemblance to a tadpole and superficially suggest the fruit of *Schizolobium* (*Cassieae*) and *Paramachaerium,* although admittedly in the latter the seminiferous area is proximal. The trees bear abundant fruits which are soon deciduous. The wood yields a bright red sap and the flowers are white. *Carcuera, tigre,* and *canela* are common names. The type of *P. maxonianum,* located at the U. S. National Herbarium, is *Pittier 5229.*

Figure 134. Platypodium elegans Vogel: A, flowering branch (× 1); B, flower (× 3); C, petals (× 2), C¹, vexillum, C², wing, C³, carina; D, androecium and receptacle (× 5); E, gynoecium and receptacle (× 5); F, fruit (× 1). A after *Hassler 7405* (MO); B-F after *Dwyer 191* (MO).

3. MACHAERIUM Pers.

Machaerium Pers., Syn. Pl. **2:** 276. 1807.

Shrubs, trees or high-climbing woody lianas, the wood yielding orange or red sap. *Leaves* imparipinnate, the leaflets few to numerous, alternate; stipelles absent; stipules often spinescent. *Racemes* axillary or terminal, these often numerous, cymoid; bracts usually small; bracteoles usually persistent. *Flowers* small, often dense, the hypanthium truncate, the teeth very short, usually truncate or obtuse; vexillum broad, usually emarginate; wing and carinal petals coherent distally along the lower margin; stamens 10, monadelphous or diadelphous and often with 2 fascicles of 5 stamens, the anthers small, usually basifixed, dehiscing longitudinally; stipe of the ovary surrounded by a glandular collar, the style slender, the stigma scarcely differentiated. *Fruits* stipitate, flat, samaroid, the seminiferous area proximal, incrassate, the wing attenuate, reticulate, the seeds variable in shape.

A genus of approximately 300 species widely distributed in the tropics of the New World and the Old World. The Panamanian species of *Machaerium* fall naturally into two groups, one with multifoliolate leaves, and the other with few leaflets. Pittier's work on *Machaerium* of Mexico and Central America (Contr. U.S. Nat. Herb. **20:** 467-477. 1922) includes six species which occur in Panama, three of which are retained here. In Panama *Machaerium* is the largest genus of the *Dalbergieae,* challenged only by *Lonchocarpus* H.B.K.

a. Fruit with the wing straight or slightly curved.
  b. Leaves with 20-80 leaflets.
    c. Leaflets palmately veined .... 1. M. chambersii
    cc. Leaflets pinnately veined.
      d. Wing of the fruit relatively thick and not drying red.
        e. Costa of the leaflets almost invisible above; seminiferous area of the fruit distinctly marginate on the upper margin ...... 2. M. glabripes
        ee. Costa of the leaflets obvious above; fruits not obviously marginate.
          f. Leaflets 20-25.
            g. Leaflets glabrous, 0.3-0.6 cm. wide; staminal sheath usually hairy distally .... 3. M. cirrhiferum
            gg. Leaflets pubescent, 1-2.5 cm. wide; staminal sheath glabrous .... 4. M. biovulatum
          ff. Leaflets 25-80, usually pubescent beneath.
            g. Unarmed trees; rachis of the leaves up to 8 cm. long; hypanthium densely aurous-puberulent; staminal sheath pubescent .... 5. M. arborescens
            gg. Armed woody vines or trees; rachis of the leaves 4-15 (-30) cm. long; hypanthium glabrous (except few hairs on the teeth); staminal sheath glabrous.
              h. Wing and carinal petals falcate; free filaments of the stamens as long as or longer than the sheath; style 1.5-3 mm. long .... 6. M. isadelphum
              hh. Wing and carinal petals not falcate; free filaments of the stamens less than half the length of the sheath; style 0.5-1.5 mm. long .... 7. M. purpurascens
      dd. Wings of the fruit paper-thin and drying red.
        e. Leaflets obtuse or rarely rounded at the apex, scarcely pubescent; hypanthium puberulent .... 8. M. capote
        ee. Leaflets rounded at the apex, densely pubescent; hypanthium glabrescent, except for scattered bulbous trichomes .... 9. M. longifolium

bb. Leaves with 5- to 16 leaflets.
c. Leaflets 5-7, long-acuminate.
d. Leaflets elliptic; flowers blue; bracteoles wider than long, not carinate; hypanthium glabrescent (except the teeth); upper margin in the wing petals straight; fruit with the wing up to 3 cm. wide, not conspicuously thickened on the lower margin ....10. M. ARBOREUM
dd. Leaflets ovate or oblong, rarely elliptic; flowers white; bracteoles at most as wide as long, carinate; hypanthium minutely puberulent; upper margin of the wing petals oblique; fruit with the wing up to 1.8 cm. wide, the lower margin 1-2 mm. thick ....11. M. DARIENSE
cc. Leaflets 6-16, not long-acuminate (except in *M. pachyphyllum*).
d. Leaflets coriaceous, long-acuminate; rachis of the leaf about 2 mm. wide; flowers about 15 mm. long ....12. M. PACHYPHYLLUM
dd. Leaflets chartaceous or membranous (subcoriaceous in *M. seemannii*), obtuse to short-acuminate; rachis of the leaf 0.5-1 mm. wide; flowers about 10 mm. long.
e. Leaflets 6-13, oblong, lanceolate or elliptic, obviously acuminate, 0.7-2 (-7) cm. wide; vexillum subcordate at the base, the claw obscure; wing petals narrowly oblong, the blade almost as wide proximally as distally; at least one filament of the stamens pubescent ....13. M. SEEMANNII
ee. Leaflets 9-11, oblong, obtuse or vaguely acuminate, 2-4 cm. wide; vexillum subcuneate at the base, the claw obvious; wing petals subrotund, the blade much wider distally than proximally; filaments of the stamens glabrous ....14. M. WOODWORTHII
aa. Fruit with the wing very broadly lunate ....15. M. LUNATUM

1. MACHAERIUM **CHAMBERSII** Dwyer, sp. nov.

Arbor?; ramuli puberuli. *Folia* 20-30-foliata, alterna, inferiora subopposita, oblongo-trapeziformia, ad 2.5 cm. longa, ad 5.5 cm. lata, apice oblique subdeltoidea et vix apiculata, basi oblique truncata manifesteque inaequilateralia, venis 3 palmatis, in sicco utrinque viridia, praeter margines glabra et papyracea; rhachides tenues, angulares et supra longitudinaliter carinati; petioli 1-10 mm. longi, glandulis basalibus 2 apice manifeste setaceis praediti; stipulae subreflexae, deltoideae, circa 3 mm. longae et 2.5 mm. latae, acutae, crassae, glabrae, spinosae vel infra coriaceae apiceque rigidiores. *Flores* non visi. *Fructus* parte seminiferente manifeste plana, oblonga, arcuata, ad 0.9 cm. longa et 0.55 cm. lata, brunnea et appresso-puberula, margine inferiore leviter bicarinato; ala cultriformis, ad 4 cm. longa et circa 1 cm. lata, apice obliqua minuteque apiculata, margine superiore vix curvato inferioreque manifeste arcuato, tenuis, in sicco rubescens, papyracea, minute puberula, venis prominulis transversis irregulariterque dispositis.

DARIEN: El Real, *Stern, Chambers, Dwyer & Ebinger 926* (MO, holotype).

I have been unable to find any species of *Machaerium* in the New World in which the secondary veins of the leaflets arise from the proximal position of the costa. Therefore I propose:

Sectio **Flabellinervata** Dwyer, sect. nov.: foliola venis secundariis flabelliformipalmatis a costae proximo parte orientibus.

Type species: *Machaerium chambersii* Dwyer.

The fruit of *M. chambersii* is strikingly like that of the Colombian *M. capote* Triana ex Dugand, reported in Panama for the first time in this paper.

The new species is named in honor of Kenneth Chambers with whom the author collected herbarium material in Panama.

2. Machaerium glabripes Pittier, Contr. U. S. Nat. Herb. **20:** 472. 1922.

Tree, small, the branchlets rimose, glabrous, armed, the spines scattered, cuneate, up to 0.3 cm. long. *Leaves* with 25-45 leaflets, these oblong, up to 1 cm. long, up to 0.3 cm. wide, truncate or obtuse at the apex, the mucro about 0.1 mm. long, obtuse at the base, the costa visible above only as an evanescent line, the principal veins numerous, irregular, evanescent above, the blade coriaceous, discolor, apparently glabrous (fide Pittier); rachises 4-7 cm. long, about 0.7 mm. wide; stipules deltoid, up to 0.3 cm. long, thin, scarious, glabrous. *Inflorescenses* unknown. *Flowers* unknown. *Fruits* pedicellate for 3-4 mm., the pedicels ferruginous-pubescent, the stipe about 8 mm. long, the seminiferous area falcately disposed, up to 2 cm. long, up to 0.5 cm. wide, turgid, obviously marginate above, glabrous, tuberculate, the tubercules striate, the wing up to 4 cm. long, up to 1.5 cm. wide, obtuse or truncate, thin, the swollen margin about 0.5 mm. wide, drying tan, glabrous or pubescent.

Known only from Panama.

coclé: Penonomé, *R. S. Williams 410* (type).

According to Pittier (loc. cit. 472. 1922), *M. glabripes* is probably related to the Colombian *M. glabratum* but unfortunately the flowers of the former are unknown.

3. Machaerium cirrhiferum Pittier, Contr. U. S. Nat. Herb. **20:** 472. 1922.

Machaerium arborescens Pittier, loc. cit. 472. 1922.
Machaerium merrillii Standley, Field Mus. Nat. Hist., Bot. Ser. **8:** 15. 1930.

Tree or trailing shrub, the trunk usually armed; branchlets terete, frequently spiral, unarmed, often tendrillous (fide Pittier). *Leaves* often ericoid, the leaflets 30-60, oblong, up to 0.7 cm. long, up to 0.35 cm. wide, obtuse, the costa evanescent above, the main veins crowded, evanescent above, prominulous beneath, the blade thin-coriaceous, subequilateral, aurous-villose proximally and marginally above, densely villose to glabrous beneath; rachises up to 8 cm. long, densely ferruginous-villose; petioles up to 1.5 cm. long; stipules lanceolate, up to 0.3 cm. long, densely villose. *Panicles* terminal or axillary, 5-40 cm. long, ferruginous-tomentose. *Flowers* with the hypanthium 5-8 mm. long, carnose, densely puberulent, the carinal tooth 1.5-2 mm. long, rounded, the vexillar teeth broader and less rounded; vexillum orbicular, about 8.5 mm. long; wing petals obliquely oblong, about 7 mm. long, rounded at the apex, oblique at the base, ciliate at the claw; carinal petals reniform, about 6 mm. long, rounded at the apex, the claw obviously eccentric, ciliate; staminal sheath about 3 mm. long, ciliate, the filaments up to 1 mm. long; ovary obviously stipitate, pilose, the style about 0.6 mm. long. *Fruits* subsessile, up to 1.6 cm. long, up to 1.5 cm. wide, the golden hairs dense, up to 1.5

cm. long, the wing cultriform, up to 3 cm. long, up to 1.7 cm. wide, obtuse, sparsely pilose.

Known only from Panama.

COCLÉ: Penonomé: *Williams 409* (type), *416* (type of *M. arborescens*); Río Las Lajas, *Allen 1606*.

The flowers of both *M. cirrhiferum* and *M. arborescens* are described as lavender. While *M. merrillii*, unlike *M. arborescens*, has stiff hairs on the seminiferous area of the fruit, it is so similar to *M. cirrhiferum* in other respects that I have not hesitated to reduce it to synonomy.

4. MACHAERIUM BIOVULATUM Micheli, Mém. Soc. Phys. Hist. Nat. Genève **34:** 265, *pl. 15.* 1903.

Machaerium acanthothrysus Pittier, Contr. U. S. Nat. Herb. **20:** 473. 1922.

Shrub or tree. *Leaves* with 9-18 leaflets, these equilateral, oblong, obovate-oblong, 2.5-8 cm. long, 1.4-2.5 cm. wide, deltoid or rounded, often emarginate, thinly coriaceous, concolor, glabrescent to moderately villulose above and below; petioles 2-4 mm. long, the rachises up to 16 cm. long; stipules erect or deflexed, up to 8 mm. long, very variable in texture and pubescence. *Panicles* terminal and up to 20 cm. long, or shorter and axillary, or disposed as several short (up to 2 cm. long) racemes in the axils, the rachis and branches aurous-puberulent, the flowers dense, subsessile or with the pedicels about 2 mm. long; bracteoles suborbicular, 1.3-3 mm. long, aurous-villulose. *Flowers* with the hypanthium up to 5.5 mm. long, aurous-puberulent, the upper teeth evanescent, the lower broadly deltoid, 0.3-1 mm. long; vexillum erect, suborbicular 8-9 mm. long, often with 2 linear callosities below the middle, aurous-villulose; wing petals falcately oblong, 8-12 mm. long, the auricle rounded, the claw curved, sparsely villose; carinal petals falcately subrotund, 7-10 mm. long, sparsely aurous-pilose; stamens monadelphous, the sheath about 7 mm. long, the filaments upright, 3-4.7 mm. long; ovary long-stipitate, falcate, densely aurous-villose, 1-ovulate, the style 3.5-4 mm. long, pubescent beneath. *Fruits* stipitate for 3-9 mm., the seminiferous area falcately oblong, 2.2-5 cm. long, about 1 cm. wide, tuberculate, the soft elongate hairs mixed with bulbous-based trichomes, the wing occasionally subhemispherical, up to 6 cm. long, obtuse, the upper margin straight, the lower curved.

Mexico and Central America.

CANAL ZONE: Las Cascadas Plantation, Summit, *Standley 29958*. COCLÉ: half mile below the village of El Valle, *Dwyer 1806*. PANAMA: Río Mamoni, *Duke 5679*.

An excellent plate (tab. 15) accompanies Micheli's original description. All pistils dissected proved to be 1-ovulate, thus calling into question the appropriateness of Micheli's specific epithet. The flowers are purple, tinged with pink, with the vexillum with a green spot within.

5. MACHAERIUM ISADELPHUM (E. Meyer) Standley, Jour. Wash. Acad. Sci. **15:** 459. 1925.

Drepanocarpus isadelphus E. Meyer, Nov. Act. Acad. Leop.-Carol. **12:** 807. 1824.
Drepanocarpus microphyllus E. Meyer, loc. cit. 808. 1824.
Nissolia aculeata DC., Prodr. **2:** 258. 1825.
Machaerium angustifolium Vogel, Linnaea **11:** 193. 1837.
Machaerium affine Benth., Comment. Legum. Gen.. 34. 1837.
Machaerium isadelphum (E. Meyer) Amshoff, Med. Bot. Mus. Herb. Rijksuniv. Utrecht **52:** 53. 1939.

Shrub, woody liana or tree; branchlets often spirally coiled, armed, the spines subulate, up to 0.4 cm. long, glabrous. *Leaves* with subsessile leaflets, these up to 80, oblong, 0.5-4.5 (-10) mm. long, 0.2-1.3 (-3) mm. wide, obtuse, mucronulate, the costa plane and subevanescent above, the blade stiff, thinly coriaceous, curled, glabrous to sparsely pilose above, minutely puberulent to pilose beneath; rachises 30-40 cm. long, ferruginous; petioles 0.5-2 cm. long, ferruginous; stipules widely subulate, up to 1 cm. long. *Panicles* terminal, up to 30 cm. long, the rachis terete, the branches arcuate, up to 3 cm. long, patulous, usually paired and subequal, subtended by reflexed spines (stipules?), the flowers 10-15 on the longer branches; bracteoles suborbicular, 1.5-3.5 mm. long, villose, with some trichomes up to 1.7 mm. long, obviously bulbous. *Flowers* with the hypanthium companulate, about 5.5 mm. long, drying purple, glabrous, the teeth scarcely evident to mammiform, 0.5-0.8 mm. long, obtuse, the upper teeth usually united, truncate, the carinal teeth narrower; vexillum reflexed, suborbicular, 6.5-10 mm. long, glabrous or villosulose; wing petals falcately oblong, 7-8 mm. long, glabrous or villosulose, subdeltoid at the apex, attenuate at the base, the auricle obvious; carinal petals obovate or subreniform, 6-7 mm. long, obtuse, the upper margin straight, the hairs few along the lower margin, the claw strongly eccentric; stamens monadelphous or diadelphous, the sheath curved, 4-5 mm. long, glabrous, the filaments more than one half the length of the sheath, the anthers about 0.6 mm. long; ovary stipitate for about 3 mm., densely sericeous, the style 1.5-3 mm. long. *Fruits* with the seminiferous area flat or scarcely turgid, falcately oblong, 1.2-5 cm. long, about 0.8 cm. wide, the wing cultriform, about 5 cm. long.

Panama and northern South America.

CANAL ZONE: Barro Colorado Island: *Shattuck 21, Woodworth & Vestal 584;* Balboa, *Standley 25500;* Cerro Gordo near Culebra, *Standley 26039;* Gamboa, *Standley 28318, 31922;* Las Cruces Trail, between Fort Clayton and Corozal, *Standley 29143;* Darien Station, *Standley 31550.* CHIRIQUÍ: Boquete, *Terry & Terry 1651.* PANAMA: Punta Paitilla, *Standley* 26233: Matías Hernández, Juan Díaz, *Standley 31975.* VERAGUAS: Santiago, *Allen 1080.*

Macbride (Field Mus. Nat. Hist., Bot. Ser. **13**(3): 276. 1943) considers the valid name of this species to be *M. aculeatum* (DC.) Raddi. Inasmuch as De Candolle (loc. cit. 258. 1825) described this as *Nissolia aculeata* in 1825, Macbride would seem to err in suggesting that Raddi effected the new combination in 1820, five years before De Candolle described the species. Unfortunately I have been unable to locate a copy of the publication (Mem. Soc. Ital. Sci. Modena **18:** 598. 1820) cited by Macbride, in which Raddi presumably effected the new combination.

Assuming that Macbride is in error, *Drepanocarpus isadelphus* and *Drepanocarpus microphyllus*, both published in 1824, would seem to have priority. Since both species were described in the same publication by E. Meyer (loc. cit. 1824), I have elected to retain the specific name *isadelphus,* as it occurs on an earlier page than *microphyllus.* The flowers are described as pale blue to lavender.

7. MACHAERIUM PURPURASCENS Pittier, Contr. U. S. Nat. Herb. **20:** 474. 1922.

Vine, woody and thorny; branchlets purple, often spirally coiled, armed, the spines few, uncinate, up to 0.3 cm. long, usually alate, puberulent. *Leaves* with 10-70 leaflets, these ovate-oblong to oblong, up to 4.5 cm. long, up to 1.3 cm. wide, obtuse and mucronulate, the costa subimmersed above, the veins numerous, pennate, evanescent above, the blade subcoriaceous, often chocolate and glabrous to sparsely pilose above, the hairs up to 1.3 mm. long, often densely aurous-pilose marginally; rachises 4-30 cm. long; petioles 1-2 cm. long, densely aurous-lanulate; stipules deltoid, 4-5 mm. long, spinoid above. *Panicles* terminal or axillary, up to 15 cm. long; bracteoles suborbicular, up to 1 mm. long. *Flowers* with the hypanthium 2-3 mm. long, drying lustrous-purple, glabrous except for the marginally puberulent teeth, the teeth scarcely evident, up to 0.8 mm. long; vexillum obreniform or subrotund, 4-4.5 mm. long, truncate or bilobed at the apex, widely auriculate at the base, sericeous on the outside; wing petals obliquely oblong or obovate-oblong, the flexure proximal, 4-5 mm. long, about 3 mm. wide; stamens disposed in 2 fascicles of 5, the sheath and the filaments subequal in length, 2-3 mm. long, the anthers up to 0.6 mm. long; ovary stipitate for 1-2 mm., about 5 mm. long, falcate, the hairs dense, short, the style up to 0.7 mm. long. *Fruits* stipitate for about 0.4 cm., the seminiferous area up to 1.5 cm. long, up to 0.7 cm. wide, moderately aurous-villosulose, the wing cultriform, up to 3.5 cm. long, about 1 cm. wide, both margins curved, drying golden-brown, moderately pilose.

Apparently restricted to Panama.

CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 316, Shattuck 817, Wetmore & Woodworth 57, Woodworth & Vestal 327, 868, 896;* east of Bella Vista, *Maxon & Valentine 63939;* Ancón, *Pittier 2749;* Fort Randolph, *Standley 28705*: Las Cascadas Plantation near Summit, *Standley 29544;* Fort Sherman, *Standley 31805;* Balboa, *Standley 32131.* COCLÉ: Penonomé, *R. S. Williams 112, 413, 414, 415.* COLÓN: France Field & Catival, *Standley 30400.* DARIEN: La Palma, *Pittier 5495.* PANAMA: Punta Paitilla, *Bro. Heriberto 215, Piper 5122;* San José Island, *Johnston 970, 1073, 1378;* Taboga Island, *Macbride 2796, Standley 27064;* Old French Cut, west of Chagres River, opposite Bohio, *Maxon 4783;* Río Tapia, *Standley 26138;* east of Río Tocúmen, *Standley 26627.* Province unknown: *Bailey & Bailey 6, Seemann 464.*

Pittier (loc. cit. 474. 1922) states that this is probably the species collected in Panama by Hayes (328) as well as by Sinclair and Hinds, and identified by Hemsley as *M. angustifolium* Vogel. The leaflets of *M. purpurascens* are larger and the inflorescences more compressed than those of *M. angustifolium.*

I. M. Johnston (Sargentia **8:** 155-156. 1949) describes in detail the spiral coiling habit of the stems, emphasizing the role of the thorns in anchoring the plants as they climb on the adjacent vegetation. The cut stems ooze a red sap;

exceptionally thick stems (3-4 cm.) usually have anomalous vascular tissues. The flowers are pink-purple.

8. Machaerium capote Triana ex Dugand, Caldasia **2:** 159, *pl.* (p. 161). 1943.

Tree variable in size; branchlets unarmed. *Leaves* up to 17 cm. long; leaflets 10-21, alternate, up to 6 cm. long, up to 2 cm. wide, often tapering abruptly to the obtuse and mucronulate tip, the costa immersed above, usually puberulent, the secondary veins about 15, the blade thinly coriaceous to chartaceous, minutely puberulent or glabrescent; petioles apparently less than 2 cm. long, slender, puberulent. *Racemes* or cymose-panicles shorter than the leaves, up to 9 cm. long; pedicels up to 5 cm. long, puberulent; bracteoles apparently briefly produced, concave, oblong-rotund, up to 1.8 mm. long, densely ferruginous-puberulent. *Flowers* with the hypanthium campanulate, about 2.5 mm. long, carnose, ferruginous-puberulent, the teeth barely visible; petals glabrous, the claws about equal to the blades; vexillum subrotund, about 7.5 mm. long; wing petals obovate-oblong, about 7.5 mm. long, obliquely rounded at the apex; carinal petals subreniform, about 6 mm. long, the claw strongly eccentric; stamens monadelphous, the filaments about equal to the sheath, the anthers about 0.2 mm. long; ovary stipitate for about 1.5 mm., densely aurous-villose, the style about 2 mm. long. *Fruits* stipitate for about 4 mm., the seminiferous area flat, falcately and narrowly oblong, about 2 mm. long, rounded or obtuse, up to 1 cm. wide, paper-thin, moderately aurous-puberulent.

Panama and Colombia (Departments of Cundamarca, Tolima, Huila and Atlántico).

darien: El Real, *Duke 5035, Stern, Chambers, Dwyer & Ebinger 890.*

These are the first records of *M. capote* in Central America. Dugand claims authorship of the species on the score that Hoehne (Fl. Bras. **25**(3): 91. 1941 and Bol. Agric. Ganaderia Dept. Atlántico **2:** 28. 1935) did not validly publish the manuscript binomial of Triana in failing to include a Latin diagnosis. While Micheli's *M. biovulatum* seems to be a close relative of *M. capote*, the latter seems more akin to *M. chambersii*, although admittedly the venation of the leaflets of the latter is strikingly different. The flowers of *M. capote* are reported as yellow or reddish.

9. Machaerium longifolium Benth., Jour. Proc. Linn. Soc. Bot. **4** (Suppl.): 55. 1860.

Machaerium costaricanum Pittier, Contr. U. S. Nat. Herb. **20:** 475. 1922.

Shrub or sprawling vine; branchlets often farinose (bases of deciduous trichomes). *Leaves* up to 17 cm. long; leaflets 22-44, narrowly oblong, up to 2 cm. long, about 1 cm. wide, acute or obtuse at the apex, the terminal cilia about 1 mm. long, the costa immersed above, the main veins crowded, evanescent beneath, the blade chartaceous to thin-coriaceous, villose, concolor; petioles up to 2 cm. long,

densely villose; rachises up to 13.5 cm. long, about 1.5 mm. wide; stipules reflexed, deltoid-subulate or uncinate, up to 10 mm. long, acute, glabrescent, indurate. *Panicles* either terminal and up to 50 cm. long, or panicles axillary and shorter, or racemes axillary, 2-6 cm. long, the flowers dense, the pedicels about 2 mm. long, puberulent; bracteoles ovate-orbicular, about 4 mm. long, the base extended as 2 callosities on the pedicel, the margin puberulent with a few, bulbous trichomes. *Flowers* with the hypanthium about 5 mm. long, carnose, rubescent and rugulose, glabrous except for a few bulbous trichomes, or occasionally the teeth marginally puberulent, the upper teeth evanescent, the 3 lower about 1 mm. long; vexillum orbicular, 8-9 mm. long, pilose on the outside; wing petals oblong, about 8 mm. long, cuneate at the base, pilose to glabrescent; carinal petals falcately oblong, about 8 mm. long, cuneate and pilose at the base; stamens in 2 fascicles of 5, the filaments less than ½ the length of the sheath, the anthers about 0.35 mm. long, subbasifixed; ovary stipitate for about 5 mm., falcate, pilose mostly on the margins, the style up to 1.5 mm. long. *Fruits* with the seminiferous area narrowly oblong, up to 1.5 cm. long, the wing cultriform, about 3 cm. long, oblique, slightly curved on both margins, chartaceous, drying tan, puberulent.

Nicaragua, Costa Rica, Panama, and apparently in northern South America.

DARIEN: El Real, Río Turia, pasture and edge of woods, *Stern, Chambers, Dwyer & Ebinger 794.*

This is the first collection of *M. longifolium* in Panama. Presumably this is the only Panamanian species of *Machaerium* with bulbous trichomes on the bracteoles and calyx. Field notes indicate that the flowers are white with green and purple markings.

10. MACHAERIUM ARBOREUM (Jacq.) Vogel, Linnaea **11:** 182. 1837.

Nissolia arborea Jacq., Enum. Syst. Pl. Carib. 27. 1762.
Nissolia glabrata Link, Enum. Pl. Hort. Bot. Berol. **2:** 221. 1822.
Machaerium acuminatum H.B.K. var. *latifolium* Benth., Jour. Proc. Linn. Soc. Bot. **4** (Suppl.): 65. 1860.
Machaerium latifolium (Benth.) Pittier, Contr. U. S. Nat. Herb. **20:** 470. 1922.
Machaerium fruticetorum Standley & Steyermark, Field Mus. Nat. Hist., Bot., Ser. **22:** 240. 1940.

Shrub or small tree; branchlets smooth, glabrous. *Leaves* with 5-7 leaflets, these elliptic to suborbicular, up to 9.5 cm. long, up to 4 cm. wide, the acumen up to 2 cm. long, the costa immersed above, the main veins about 7, immersed above, the blade chocolate beneath, glabrous to glabrescent; petioles 3-4 cm. long, glabrous; rachises about 6 cm. long. *Panicles* several per axil, up to 9 cm. long, the branches up to 3 cm. long; bracteoles broadly reniform, up to 3 mm. wide, pilulose above on the outside, sericeous within above the attachment scar. *Flowers* with the hypanthium up to 5.5 mm. long, ribbed, glabrescent below, minutely puberulent on the teeth, the latter subequal, deltoid to oblong, up to 1 mm. long, the carinal tooth much narrower; vexillum broadly obovate-deltoid, up to 9 mm. long, up

to 13 mm. wide, truncate at the base, densely aurous-pilose on the outside; wing petals oblong-rectangular, up to 8 mm. long, scarcely tapering at the base, sacculate-auriculate, aurous-pilose proximally; carinal petals sublunate, about 7.5 mm. long, densely pilose along the lower margin and at the middle, the short claw strongly eccentric; stamens monadelphous, the anthers 0.7-1.5 mm. long; ovary stipitate for about 2.5 mm., densely aurous-sericeous, the style 2-2.5 mm. long, curved. *Fruits* with the wing narrowly falcate or inequilaterally oblong, up to 8 cm. long, up to 1.8 cm. wide, obtuse or cuneate at the apex, apparently glabrous.

Mexico, Honduras, Costa Rica, and Panama.

CANAL ZONE: Barro Colorado Island, *Brown 177, Dodge 3480;* Tumba Vieja and Salamanca, *Steyermark & Allen 16746.*

Although the fruits of the Mexican, Costa Rican, and Honduras material of *M. latifolium* reach 10 cm. in length and 2.5 cm. in width, and thus seem larger than those of typical *M. arboreum,* there appears to be no substantial grounds for segregating *M. latifolium* as a distinct species. Material of *M. pittieri* Macbr., while bearing a close resemblance to *M. arboreum,* shows important floral differences; the claw of the wing petals of *M. arboreum* is attached submedianally at the base of the blade, whereas the claw in *M. pittieri* is strongly eccentric; in the former species the lower margin of the blade of the wing petals is rounded while in *M. Pittieri* it is strongly curved. The flowers of *M. arboreum* are described as blue.

11. MACHAERIUM DARLENSE Pittier, Contr. U. S. Nat. Herb. **20:** 470. 1922.—Fig. 135.

Tree, scandent in habit, or shrub. *Leaves* with 4-7 leaflets, these subelliptic, ovate or obovate-oblong, 4-14 cm. long, 1.5-7 cm. wide, long-acuminate, the costa immersed above, the main veins 6-16, stiff-chartaceous to subcoriaceous, equilateral, reticulate, glabrous above, pubescent along the costa below; petioles up to 3.5 cm. long; rachises 3-9.5 cm. long; stipules cuneate, up to 0.7 cm. long, cleft, curved. *Panicles* axillary or terminal, up to 8 cm. long, the branches often paired, up to 2 cm. long, wiry, sharply ascending, the flowers densely capitate; bracts ovate, up to 3 mm. long; bracteoles orbicular, up to 2 mm. long, the hairs short and rigid. *Flowers* with the hypanthium 5-6 mm. long, puberulent mostly on the teeth, the latter scarcely discernible, or up to 1 mm. long, very broad at the base; vexillum orbicular, about 7 mm. long, cuneate at the base, the short claw densely puberulent; wing petals falcately oblong, about 8 mm. long, the auricle about 1 mm. long, the lower margin strongly curving, narrower and arcuate near the claw, densely aurous-villose proximally especially below the middle, the claw obviously eccentric; carinal petals subreniform, about 8 mm. long, venose, carnose, densely villose along the lower margin, the claw obviously eccentric; stamens monadelphous or diadelphous, the filaments longer than the sheath, the anthers 0.5-0.6 mm. long; ovary stipitate for about 4 mm., aurous-villose, the style 0.8-1.8 mm. long. *Fruits* stipitate for about 7 mm., the stipe ferruginous-puberulent, the seminiferous

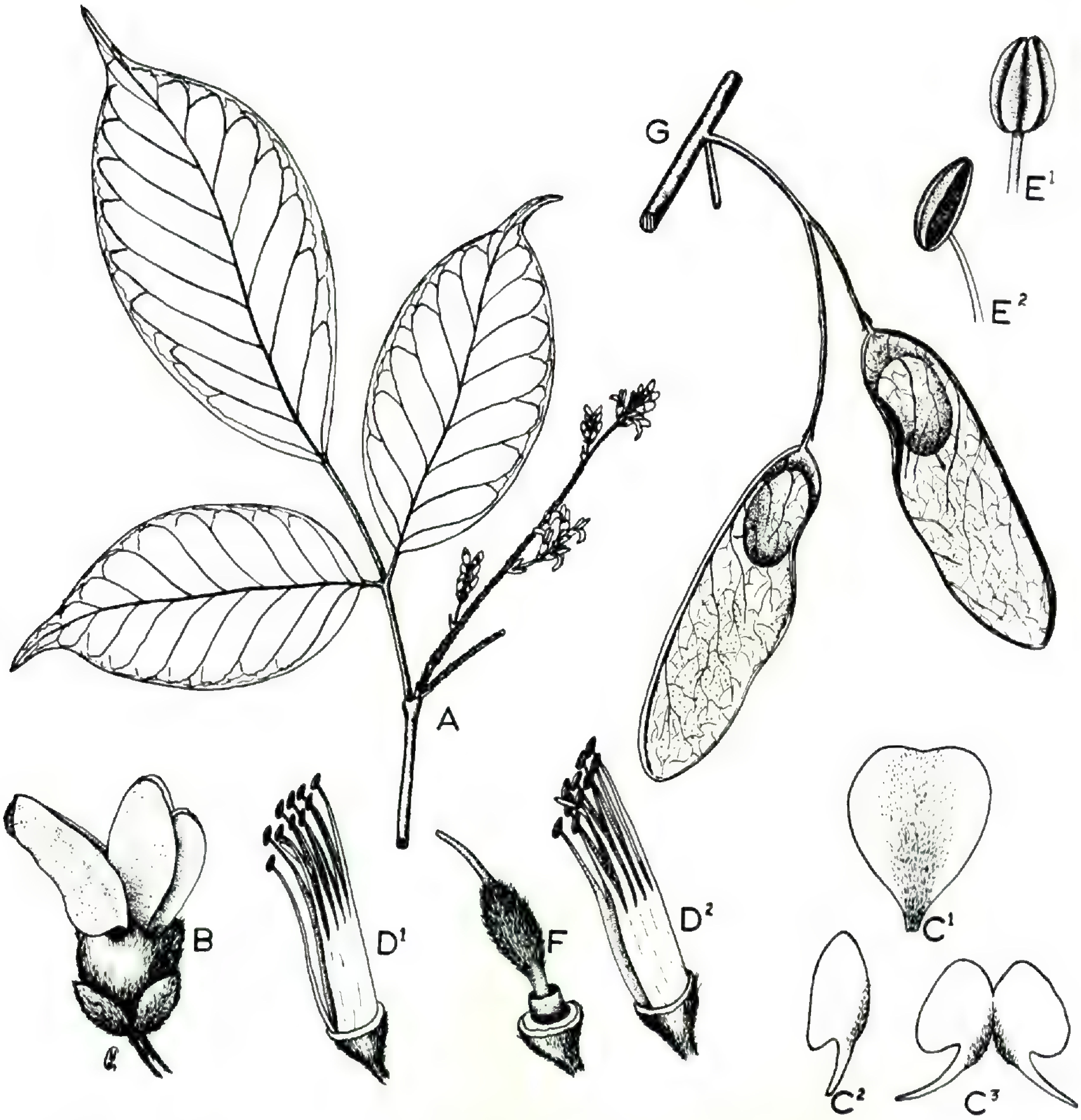

Figure 135. MACHAERIUM DARIENSE Pittier: A, flowering branch (× 1); B, flower (× 7); C, petals (× 5), C[1], vexillum, C[2], wing, C[3], carina; D, androecium (× 10), D[1], diadelphy, D[2], monadelphy; E, stamens (much enlarged), E[1], anther showing dehiscence, E[2], anther showing filament attachment; F, gynoecium and receptacle (× 10); G, fruit (× 1). After *Skutch 4795* (MO).

area about 2.5 mm. long, about 1.3 cm. wide, flat, not strongly falcate, the wing cultriform, 4-9 cm. long, 1-2.6 cm. wide, oblique with the ventral margin broadly contracted toward the base, the dorsal margin 1-2 mm. wide, reticulate, glabrous or sparsely villosulose.

Costa Rica and Panama.

CANAL ZONE: Barro Colorado Island, *Killip 40014*. DARIEN: La Palma, *Pittier 5497* (type).

The flowers are described as white.

12. Machaerium pachyphyllum Pittier, Contr. U. S. Nat. Herb. **20:** 469. 1922.

Machaerium marginatum sensu Johnston, Sargentia **8:** 154. 1949, non Standley, Jour. Wash. Acad. **14:** 95. 1924.

Tree, small, or sprawling shrub or woody vine; branchlets well armed, the spines subulate, 0.5-1.5 cm. long, uncinate, often only the bases persistent. *Leaves* with 14-17 leaflets, these ovate to oblong, 3.5-18 cm. long, 1.8-6 cm. wide, the acumen up to 2.5 cm. long, the costa immersed above, the blade glabrous to densely ferruginous-puberulent, coriaceous, lustrous above, the margin often vaguely irregular; petioles stout, 7-8 cm. long, the indumentum variable; rachises up to 17 cm. long. *Panicles* axillary or terminal, up to 60 cm. long, the branches unequal, several per axil, up to 16 cm. long; bracteoles orbicular, about 5.5 mm. long. *Flowers* about 15 mm. long, the hypanthium about 8 mm. long, densely tomentose, the teeth unequal, deltoid, 1.8-3 mm. long, the carinal tooth usually longer and thicker; vexillum orbicular, about 12 mm. long, densely puberulent; wing petals falcately oblong, about 14 mm. long, glabrous; carinal petals falcately oblong, usually shorter and narrower than the wing petals, obviously rostrate, glabrous; filaments up to 3.3 mm. long, the anthers about 0.5 mm. long; ovary stipitate for 2-5 mm., 3-4.5 mm. long, densely villosulose. *Fruits* with the seminiferous area oblong, up to 2 cm. long, about 1 cm. wide, aurous-puberulent with longer trichomes interspersed, the wing up to 2 cm. long, about 2 cm. wide, obtuse, reticulate, glossy, glabrescent to sparsely villosulose with a few trichomes persistent.

Costa Rica and Panama.

canal zone: Barro Colorado Island, *Kenoyer 6721, Standley 40865, Wilson 78, Woodworth & Vestal 349;* Chiva-Chiva Trail, *Piper 5714;* Las Cascadas Plantation, *Standley 25721, 29614;* Gamboa, *Standley 28382,* Fort Sherman, *Standley 31059;* Obispo, *Standley 31791.* coclé: Penonome, *R. S. Williams 397.* panama: Panama City, *Bro. Paul 418;* San José Island, *Johnston 419, 769.*

The material which I have seen in American herbaria labelled *M. marginatum* is *M. pachyphyllum;* the type of the latter is *R. S. Williams 170* from El Salvador. The leaves of *M. marginatum* are considerably larger, the bracteoles are oblong and have bulbous trichomes, and the flowers are only two thirds the length of those of *M. pachyphyllum.* The wing of the fruit of *M. pachyphyllum* is not obviously curved on either margin, in this respect differing from the fruits of those species of *Machaerium* in Panama with wide leaflets.

The flowers of *M. pachyphyllum* are reported to be white and tinged with red. I. M. Johnston (Sargentia **8:** 155. 1949) remarks on the climbing habit of *M. pachyphyllum* (*M. marginatum* sensu Johnston) on San José Island, the pole-like stems, which may be readily observed on Navy Road and at Marino, shedding their leaves in the middle of January, with the flowers appearing about a month later.

13. Machaerium seemannii Benth. ex Seem., Bot. Voy. Herald 110. 1853.

Machaerium campylocarpum J. D. Sm., Bot. Gaz. **44:** 109. 1907.

Liana, giant and woody, or spreading shrub. *Leaves* with 6-13 leaflets, these

oblong-lanceolate, ovate, elliptic or oblong, 1.5-7.5 cm. long, 0.7-2.7 cm. wide, the acumen narrow and falcate, the costa plane or immersed above, the main veins 15-20, the blade thinly coriaceous, lustrous and dark-green above, usually sparsely pilose on the costa and margins; petioles 2-3 cm. long; rachises 5-5.8 cm. long. *Panicles* compressed, axillary, up to 5 cm. long, the shorter branches 3-7 per axil, puberulent and rough with persistent bracts, the latter rotund, up to 1 mm. long, densely puberulent; bracteoles subreniform, about 1.5 mm. long, puberulent. *Flowers* 5-20 per branch, distichous, the hypanthium shallow, 3-3.5 mm. long, densely puberulent, the teeth (except for the carinal tooth) evanescent; vexillum orbicular-oblong, about 8 mm. long, vaguely auriculate, appressed-sericeous, the claw about 6 mm. long; wing petals narrowly falcate, about 8 mm. long, densely aurous-villose on the outside; carinal petals subrotund, about 8.5 mm. long, aurous-villose; stamens monadelphous, the filaments about ½ the length of the sheath, villose (at least the median), the anthers 1-1.3 mm. long; ovary stipitate for about 2.5 mm., densely aurous-villose, the styles subulate, about 2 mm. long, pubescent toward the base. *Fruits* stipitate for about 0.7 cm., the seminiferous area usually turgid, up to 2 cm. long, up to 0.9 cm. wide, the wing cultriform, up to 4.5 cm. long, up to 2 cm. wide, reticulate, the veinlets prominulous, minutely aurous-puberulent, often powdery in appearance, the carinal margin about 1.5 mm. wide.

Honduras, Guatemala, Panama and Colombia.

CANAL ZONE: Gatun Lake, *Bangham 435;* Quebrada La Palma & Río Chagres, *Dodge & Allen 17347;* Barro Colorado Island, *Killip 40010, Shattuck 126, Standley 31248, 40942, Wetmore & Woodworth 51, 60;* Frijoles, *Piper 5791;* Las Cascadas Plantation, *Standley 25703, 29624;* Corozal, *Standley 27348, 29135;* Río Tapía, *Standley 28130;* Fort Sherman, *Standley 31025;* Darien Station, *Standley 31613.* CHIRIQUÍ: El Boquete, *Davidson 733, Terry & Terry 1626;* Cerro Vaca, *Pittier 5310.* COCLÉ: Paso del Adrado & Ola, *Pittier 5094.* COLÓN: France Field and Catival, *Standley 30293.* DARIEN: Río Chico, *Allen 4604.* PANAMA: San José Island, *Johnston 1328.*

The unique condition in *M. seemannii* of having one or more filaments of the stamens villose is noteworthy. Presumably the flowers vary from blue to black. I. M. Johnston (Sargentia **8:** 156. 1949) notes that the stems of his collection (1358) "oozed no gory juice," an unusual deficiency of the vascular tissue of a species of *Machaerium.*

14. MACHAERIUM WOODWORTHII Standley, Contr. Arnold Arb., **5:** 81, *pl. 12.* 1933.

Tree (?), the twigs unarmed. *Leaves* imparipinnate; leaflets 9-11, alternate, oblong, up to 6 cm. long, 2-4 cm. wide, obtuse and vaguely acuminate, the costa immersed above, the main veins about 10, plane above, curving near the callose and subundulate margin, the blade chartaceous, concolor, minutely aurous-puberulent beneath; petiolules about 3 mm. long; petioles 3-4 cm. long; rachises 4-9 cm. long. *Panicles* axillary, 4-5 cm. long; bracteoles subtrapeziform, about 1.3 mm. long, obtuse, densely puberulent. *Flowers* sessile, the hypanthium urceolate, about 4 mm. long, aurous-puberulent, the teeth up to 0.5 mm. long, broadly obtuse; vexillum obovate-oblong, about 6.5 mm. long, about 4 mm. wide, rounded at the

tip, cuneate at the base, narrowly and abruptly flexed near the middle, glabrous; carinal petals subreniform, about 5 mm. long, the claw eccentrically attached, glabrous; stamens monadelphous, the filaments about ½ the length of the sheath, the anthers about 0.4 mm. long; pistil stipitate for about 2 mm., densely aurous-puberulent, the style about 0.8 mm. long. *Fruits* unknown.

Native to Panama.

CANAL ZONE: Barro Colorado Island, *Woodworth & Vestal 422* (type).

Standley's remark (Carnegie Inst. Wash. Publ. **461:** 64. 1935), that his *M. rosescens* (type *Schipp 1091*, from British Honduras) is closely related to *M. woodworthii*, is noteworthy, but difficult to evaluate, in view of the paucity of material.

15. MACHAERIUM LUNATUM (L. f.) Ducke, Arch. Jard. Bot. Rio de Janeiro **3:** 151. 1922.

Pterocarpus lunatus L. f., Suppl. Pl. Syst. Veg. 317. 1781.
Drepanocarpus lunatus (L. f.) G. F. W. Meyer, Prim. Fl. Essequeboensis 238. 1818.

Shrub, woody vine, shrub or tree, the branchlets armed. *Leaves* with 8-20 leaflets, these oblong, 1.5-3.5 cm. long, 0.8-2 cm. wide, obtusely truncate, thin-coriaceous, glabrous at maturity, the costa often immersed above, the main veins crowded; petioles 1-2.5 cm. long; rachises 2-5 cm. long. *Panicles* terminal, up to 15 cm. long; stipules spiniform, subulate, up to 1 cm. long, reflexed, glabrous toward the tip; pedicels about 2 mm. long; bracteoles orbicular, 1.5 mm. long. *Flowers* with the hypanthium about 5 mm. long, glabrous to puberulent, venose within, the teeth evanescent, about 0.6 mm. long; vexillum subrotund, broader than long, about 7.5 mm. wide, villosulose, shortly auriculate at the base, the claw about 3.5 mm. long; wing petals oblong, about 8 mm. long, obtuse, truncate at the base; carinal petals subreniform, about 9 mm. long, glabrous; stamens monadelphous, the filaments about ½ the length of the sheath, the anthers about 0.65 mm. long, scarcely wider than the filaments; ovary stipitate for about 6 mm., densely sericeous to glabrescent, falcately oblong, the style about 3 mm. long. *Fruits* strongly lunate (appearing orbicular), 2-3 cm. long, 2-3 cm. wide, flat, rugulose, moderately puberulent.

Central America, West Indies, tropical South America and Africa.

CANAL ZONE: hills west of the Canal near Gatun, *Standley 27292;* Fort Randolph, *Standley 28693;* Darien Station, *Standley 31616.* CHIRIQUÍ: David, *Pittier* 3373. PANAMA: Mamoni River, *Pittier 4585.*

As the specific name suggests *M. lunatum* is readily recognized by its strongly curved fruits. The flowers are described as lilac or purple.

4. PARAMACHAERIUM Ducke

PARAMACHAERIUM Ducke, Arch. Jard. Bot. Rio de Janeiro **4:** 86. 1925.

Trees. Leaves imparipinnate; leaflets several, alternate, penni-nerved; stipules minute, soon deciduous. *Panicles* terminal, multi-flowered; bracts persisting; brac-

Figure 136. PARAMACHAERIUM GRUBERI Brizicky: A, leaf (× ½); B, fruit (× ½). After *Gruber s. n.* (MO, isotype).

teoles often much larger than the bracts. *Flowers* with the hypanthium campanulate, somewhat gibbous and bilabiate, obtuse at the base; vexillum distinctly clawed; carinal petals coherent; stamens 10, monadelphous, the anthers versatile; glandular disk present; ovary scarcely stipitate, the stigma capitate, the ovules several. *Fruits* sessile, the seminiferous area basal, turgid, the seeds several.

A genus of three species, one found in Panama, one in British Guiana and in the territory of Río Branco, Brazil, and the third in the States of Pará and Amazonas, Brazil.

1. PARAMACHAERIUM GRUBERI Brizicky, Trop. Woods **112**: 58. 1960.—Fig. 136.

Tree up to 30 m., the sap red. *Leaves* up to 27 cm. long, the leaflets 9-13, alternate, oblong, the apical oblanceolate or obovate, the basal lanceolate or ovate, 5-13 cm. long, 2-4.5 cm. wide, acuminate, the main veins about 14. *Panicles*

terminal, the rachis slender, up to 5 cm. long, tomentose. *Flowers* with the hypanthium tubular-campanulate, about 7.5 mm. long, carnose, densely pilulose within, the 3 lower teeth deltoid, about 2 mm. long, acute, the upper 2 united along most of their length, a little longer than the lower; vexillum suborbicular, about 9 mm. long; wing petals suborbicular, up to 8 mm. long, tapering more sharply along the upper margin; carinal petals gibbous, obovate-falcate, about 5 mm. long; stamens monadelphous, the sheath open above, up to 3.5 mm. long, the linear-subulate filaments up to 2.5 mm. long, the carinal filament free almost to the base of the sheath, the anthers about 0.5 mm. long, versatile; ovary apparently sessile, terete or more compressed above the middle, ferruginous-villose, the hairs more dense above the middle on the carinal side, 4- to 5-ovulate, the style about 3.5 mm. long, thickly subulate, glabrous. *Fruits* sessile, glabrous, the seminiferous area often plump, obliquely subrotund, occupying about one third of the length of the fruit, thickened, woody, strongly veined, lustrous, the wing cultriform, about 7.5 cm. long, up to 4.5 cm. wide, rounded, very thin, flat, the upper margin scarcely curved, the lower curved; seeds 4-5, separated by obvious septa, flat, lanceolate-oblong, about 2 cm. long, about 0.5 cm. wide, oblique and beaked.

Known only from Panama.

CHIRIQUÍ: Puerto Armuelles, *Gruber s. n.* (type), *Stern & Chambers 132.*

Brizicky, in his lengthy discussion of this species, favors relating *Paramachaerium* to *Machaerium*, rather than to *Pterocarpus* L. If, however, the wing of *Paramachaerium* were cut away, leaving a stump at the seminiferous area, it would be difficult to distinguish the fruits of the two genera. Of interest is the fact that the carinal stamen of *Paramachaerium* is more free of the sheath than are its companions, a character known to mark some of the species of *Pterocarpus*.

5. CENTROLOBIUM Mart. ex Benth.

CENTROLOBRIUM Mart. ex Benth., Comment. Legum. Gen. 31. 1837.

Trees, unarmed. *Leaves* alternate, imparipinnate, the leaflets several, opposite or subopposite, the glandular-lepidote blades with the costa immersed or subprominulous; stipules inequilaterally ovate. *Panicles* terminal, densely flowered; bracteoles located above the middle of the pedicel. *Flowers* with the hypanthium subturbinate to campanulate, the upper teeth united, obtuse, the lower teeth acute; vexillum broadly ovate or orbicular; stamens 10, monadelphous, the sheath open above, the anthers versatile; ovary stipitate, the stipe rarely surrounded by a disk, the ovules 2-3, the style slender, curved, the stigma capitate. *Fruits* large, samaroid, indehiscent, the seminiferous area proximal, bearing a stylar spine, venose, glandular-lepidote; seeds subreniform, separated by transverse or oblique partitions.

A small tropical genus limited to Panama and northern South America. One species is introduced into Africa.

a. Leaflets 9-21, mostly ovate-oblong, up to 6 cm. wide; hypogynous disk absent; fruit with the stylar spine scarcely free from the body of the wing ....1. C. YAVIZANUM

aa. Leaflets 7-15, mostly ovate-elliptic, up to 14 cm. wide; hypogynous disk evident; fruit with the stylar spine free from the body of the wing ....2. C. PARAENSE var. ORINOCENSE

1. CENTROLOBIUM YAVIZANUM Pittier, Jour. Wash. Acad. Sci. **5:** 469. 1915.—Fig. 137.

Tree, the branchlets terete, densely pubescent and obviously orange-lepidote.

Figure 137. CENTROLOBIUM YAVIZANUM Pittier: A, leaf (× 1), B, flower (× 5); C, petals (× 4), C^1 vexillum, C^2, wing, C^3, carina; D, androecium (monadelphy) and receptacle (× 7); E, stamens (× 25), E^1, versatile and dehiscent anther, E^2, anther showing dehiscence; F, pistil and receptacle (× 10); G, fruit and persistent calyx (× 1); H, spine of fruit (× 3). A after *Stern, Chambers, Dwyer & Ebinger 761* (MO); B-H after *Stern, Chambers, Dwyer & Ebinger 761A* (MO).

Leaves with 9-21 leaflets, these oblong or ovate-oblong, 5-13 cm. long, about 6 cm. wide, briefly acuminate, chartaceous to thin-chartaceous, moderately villosulose especially on costa and veins, densely orange-lepidote below, the costa immersed or subprominulous, tapering markedly toward the apex; petioles 6-10 cm. long, up to 0.4 cm. wide, densely puberulent; stipules orbicular, membranous, villose. *Panicles* terminal, up to 50 cm. long, the branches arcuate, densely puberulent, orange-lepidote; bracteoles flat, rotund, about 1 mm. long, carnose, puberulent. *Flowers* with the hypanthium gibbous, campanulate, about 8 mm. long, carnose, glabrous but ferruginous-villosulose at the tips of the teeth, the upper teeth united almost to the apex, about 4 mm. long, the carinal tooth suborbicular, about 4.5 mm. long, and 4 mm. wide; vexillum strongly reflexed, obovate-oblong, about 11 mm. long, broadly cuneate at the base, the claw carnose; wing and carinal petals subequal, obovate-oblong, about 15 mm. long, about 4 mm. wide, gibbous proximally along the upper margin, the auricles small, carnose, glabrous, the claw short; carinal petals falcately and narrowly oblong, about 11 mm. long, about 4 mm. wide, the lower margin tapering to the base, the upper margin gibbous at the base, the auricles about 1.5 mm. long, rounded; stamens monadelphous, the sheath about 4 mm. long, about 3 mm. wide near the base, about 1.7 mm. wide near the apex, glabrous, the filaments subulate, about 1.5 mm. long, the anthers about 1 mm. long. *Fruits* stipitate for about 2.5 cm., the stipe with a few subulate spines up to 0.3 cm. long, the seminiferous area turgid, subrotund, about 4 cm. long, the spines 1.2-1.8 mm. long, about 0.5 mm. wide, the wing cultriform, up to 10 cm. long, scarcely wider at the apex than at the base, the upper proximal portion elevated above the seminiferous area for about 1.2 cm., the stylar spine oblique, up to 1.2 cm. long, carrying the wing almost to its apex, the wing thin, glandular-lepidote, densely puberulent, the upper margin straight, the lower margin arcuate, the veins delicate, broadly arcuate; seeds usually solitary, oblong, about 0.6 cm. long, contorted, hard, smooth, lustrous, drying yellow.

Known only from the Province of Darien, Panama.

DARIEN: Yaviza, *Pittier 6572;* El Real, *Stern, Chambers, Dwyer & Ebinger 731, 761, 761A.*

The collections of Stern, Chambers, Dwyer & Ebinger cited above, were made from a solitary tree in a pasture adjacent to the airport at El Real. Laden with flowers (as well as with green fruits in all stages of development), it provided material for the first adequate description of the blossoms. Especially noteworthy is the absence of a hypogynous disk in the flowers.

In botanizing on the banks of the river at the type locality of Yaviza, a few miles from El Real, we found abundant fruits of *C. yavizanum*. It is known as *amarillo de Guayaquil* and is sought by lumbermen.

2. Centrolobium paraense Tul. var. orenocense Benth. in Mart., Fl. Bras. **15:** (1):266. 1862.

Centrolobium patinense Pittier, Jour. Wash. Acad. Sci. **5:** 470. 1915.
Centrolobium orinocense (Benth.) Pittier, Bol. Técn. (Min. Agric. Cria) Serv. Bot. (Caracas) **5:** 123. 1944.

Tree, tall. *Leaves* with 7-15 leaflets, these ovate to elliptic, 11-24 cm. long, 6-16 cm. wide, obtuse and often abruptly and shortly acuminate, rounded to subcordate at the base, glabrescent to glabrous, the margin lightly revolute, the blade orange-lepidote. *Inflorescences* unknown. *Flowers* not seen; hypogynous disk present. *Fruits* with the seminiferous area turgid, subglobose, up to 5 cm. long, the spines dense, linear-subulate, up to 3 cm. long, moderately stiff, the wing cultriform, up to 20 cm. long, up to 8 cm. wide, obliquely truncate to obliquely rounded at the apex, the upper margin slightly curved, the stylar spine almost entirely free from the wing, up to 1 cm. long, the veins numerous, prominulous, curving sharply toward the lower margin.

Known from Panama, British Guiana, Brazil, and Ecuador.

DARIEN: Patino, *Pittier 6611* (type of *C. patinense*).

6. PTEROCARPUS L.

PTEROCARPUS Jacq., Sel. Stirp. Am. Hist. 283. 1763.

Moutouchi Aubl., Hist. Pl. Gui. Fr. 748. 1775.
Pterocarpus L. sect. *Moutouchia* (Aubl.) DC., Prodr. **2**: 418. 1825.
Pterocarpus sect. *Echinodiscus* DC., loc. cit. 418. 1825.
Echinodiscus (DC.) Benth., Comment. Legum. Gen. 30. 1837.
Moutouchia Aubl. corr. Benth., loc. cit. 30. 1837.
Phellocarpus Mart. ex Benth., loc. cit. 42. 1837.
Ancylocalyx Tul., Ann. Sci. Nat., Bot., ser. 2, **20**: 136. 1843.

Trees, unarmed. *Leaves* alternate, imparipinnate; stipules usually minute. *Flowers* in axillary or terminal racemes or panicles; bracts and bracteoles small and caducous, or large and lanceolate; hypanthium campanulate, the teeth minute; stamens monadelphous or diadelphous, the sheath open above, occassionally below, the filaments short, the anthers versatile; ovary sessile or obviously stipitate, the style slender, the stigma terminal, minute. *Fruits* orbicular or oval-oblong, flat, the seminiferous area median, the wing membranous to coriaceous, disposed in an elliptic, falciform or circular fashion, rarely rudimentary, the seeds usually solitary.

A large pantropical genus of about 60 species, a third of which are in tropical Africa.

a. Hypanthium aurous-puberulent; ovary appressed-pilose.
  b. Leaflets 5-9; teeth of the calyx 1-2 mm. long; claw of the vexillum about 4.5 mm. long; ovary uniformly oblong .... 1. P. HAYESII
  bb. Leaflets 8-14; teeth of the calyx up to 0.5 mm. long; claw of the vexillum scarcely evident; ovary rotund at the base, narrowly oblong above .... 2. P. BELIZENSIS
aa. Hypanthium essentially glabrous; ovary glabrous .... 3. P. OFFICINALIS

1. PTEROCARPUS HAYESII Hemsl., Diag. Pl. Nov. Mex. Centr.-Am. 8. 1878.

Pterocarpus reticulatus Standley, Trop. Woods **16**: 38. 1928.

Tree up to 80 feet high. *Leaves* with 5-9 leaflets, these ovate or oblong, 6-13 cm. long, 3-6 cm. wide, the acumen vague or up to 1.5 cm. long, the margin crisp,

the blade thin-coriaceous, glabrous or pubescent, the costa prominulous above, the main veins 6-10; petioles 3-9 cm. long; rachises 4-19 cm. long, aurous-tomentulose. *Inflorescences* exceeding the uppermost leaves; pedicels 0.5-1.0 cm. long, slender. *Flowers* with the hypanthium obliquely urceolate or turbinate, 5-11 mm. long, aurous-puberulent, the teeth subequal, 1-2 mm. long, often the upper truncate, the 3 lower deltoid; vexillum oblong-rotund, 13-16 mm. long, glabrous; wing petals falcately oblong, up to 11 mm. long, the auricle subrotund, the claw about 5 mm. long; carinal petals subtrapeziform, up to 12.5 mm. long, about 3 mm. wide, puberulent along the upper margin, the claw about 2.5 mm. long; stamens monadelphous, the sheath about 4.5 mm. long, glabrous, the filaments variable, up to 7.5 mm. long, those with aborted anthers slender, those with functional anthers carnose and appressed-pilose; style slender, up to 10 mm. long. *Fruits* scarcely stipitate, oval, up to 6 cm. long, up to 5.5 cm. wide, membranous, winged, drying golden-tan, the numerous delicate veins arising flabellately from the base.

British Honduras, Nicaragua, Guatemala, Costa Rica, and Panama.

BOCAS DEL TORO: Almirante, *Cooper 573;* Western River, Chiriquí Lagoon, *von Wedel 775.* CANAL ZONE: Barro Colorado Island, *Bangham 502, Chickering 57, Carpenter 45, 59, 63, Kenoyer 394, Salvoza 928, Shattuck 698, Standley 40869.* DARIEN: Patino, *Pittier 6612.* PANAMA: Arraiján, *Allen 2146;* Mamoni River, *Pittier 7000.*

P. hayesii is beautifully figured in Hemsley, Biol. Centr.-Am. **5:** *pl. 17.* 1888. Its densely puberulent calyx readily distinguishes it from the more common *P. officinalis* Jacq. The type collection, *Hayes 597,* which I have not seen, was reported as being collected near Matachin, Province of Panama. The common name is *bloodwood,* the sap being intensely red.

2. Pterocarpus belizensis Standley, Trop. Woods **7:** 6. 1926.

Tree, small, the buttresses narrow and fluted, the trunk somewhat angular. *Leaves* with 8-14 leaflets, these oblong, up to 20 cm. long, up to 7 cm. wide, the acumen up to 1.5 cm. long, thinly coriaceous, glabrous, the main veins prominulous, branching near the margin, the margin scarcely thickened, irregular, occasionally with small glands (teeth); petiolules subturgid, about 0.8 cm. long; rachises terete; petioles swollen basally for about 1 cm., up to 15 cm. long. *Panicles* apparently terminal, up to 25 cm. long, the branches well-spaced, 4-5 cm. long, recurved, puberulent, 10 to 20 flowered; pedicels slender, about 0.4 cm. long, the pedicellar scars alternate. *Flowers* about 15 mm. long, the hypanthium urceolate, about 5 mm. long, minutely puberulent, the teeth subequal, deltoid, up to 0.5 mm. long; vexillum orbicular, about 13.5 mm. long, emarginate, glabrous, the basal auricle obtuse, about 0.3 mm. long, the claw up to 1.5 mm. long; wing petals narrowly oblong, up to 11.5 mm. long, the auricles obtuse, glabrous; carinal petals free, oblong-oval, longer than the wing petals, about 13 mm. long, obliquely truncate at the base, the upper auricle somewhat larger than the lower, the claw about 4 mm. long, minutely puberulent; stamens monadelphous, the sheath flat, about 5 mm. long, the filaments variable in length, the lateral ones almost as long as the sheath, glabrous, the anthers about 1 mm. long; ovary short-stipitate, flat, subrotund at the base, narrowly oblong

above, about 5 mm. long, about 1.3 mm. wide at the base, villosulose, the style subulate, about 2 mm. long. *Fruits* suborbicular, up to 8 cm. long, drying tan, the seminiferous area turgid at maturity, the wing paper-thin, glabrous.

Known from British Honduras and Panama.

BOCAS DEL TORO: Almirante, *Cooper 496.* CANAL ZONE: Las Cascadas, *Sianca 310.*

P. belizensis appears to be more closely related to *P. hayesii* than to *P. officinalis.* Two floral characters immediately segregate it from both of these: the shortly clawed vexillum and the basally rotund ovary. The floral description given above is based on Sianca's collection (*310*) in the U. S. National Herbarium. The common names of the species are *cricamola* and *kaway.* The type is *Record 12* from British Honduras.

3. PTEROCARPUS OFFICINALIS Jacq., Sel. Stirp. Am. Hist. 283. *t. 183, fig. 92.* 1763. —Fig. 138.

Pterocarpus draco L., Sp. Pl. ed. 2, 1662. 1763, pro parte.
Moutouci suberosa Aubl., Hist. Pl. Gui. Fr. 748. *t. 299.* 1775.
Pterocarpus suberosa (Aubl.) Pers., Syn. Pl. **2**: 277. 1807.

Trees, medium-sized to large. *Leaves* with 8-12 leaflets, these alternate, ovate-oblong to oblong, 7.5-15 cm. long, 3.5-7 cm. wide, the acumen falcate, up to 2 cm. long, vaguely decurrent on the petiolule, chartaceous to thinly coriaceous, lustrous, reticulate, glabrous, the costa plane or immersed above, the main veins 10-20, arcuate, the margin somewhat crisp; petioles 2.5-7 cm. long, swollen basally; rachises up to 17 cm. long. *Panicles* terminal, often equal to the leaves in length, the rachises up to 0.3 cm. wide at the base, drying black, scattered ferruginous-villose, the lowermost branches spreading, up to 7 cm. long, the flowers mostly persistent at the tips of the branches; bracts lanceolate, about 2 mm. long, the bracteoles up to 0.6 mm. long; pedicels slender, about 3 mm. long. *Flowers* with the hypanthium turbinate, about 1.3 mm. long, thickly carnose, glabrous; vexillum reflexed, suborbicular to obreniform-orbicular, about 8 mm. long, glabrous, the claw cuneate, up to 5 mm. long; wing petals obliquely rotund, up to 11.5 mm. long, up to 6 mm. wide, truncate at the base, glabrous, the claw about 4 mm. long; staminal sheath 2.5-4 mm. long, about 0.7 mm. wide, glabrous, the filaments often slightly longer than the sheath, the anthers about 0.5 mm. long; ovary stipitate for 3.5 mm., about 3 mm. long, glabrous, the subulate style up to 2.5 mm. long. *Fruits* stipitate for about 3 mm., flat, the winged body inequilateral, subrotund, oblong or ovate, 2-5 cm. long, 3-3.5 cm. wide, obtuse to acuminate at the apex, very oblique at the base, smooth, lustrous, the veins usually prominent and flabellate.

P. officinalis is widely distributed in Central America, in the Antilles, and in many parts of northern South America.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 128;* Punta Rovalo to Rovalo River, Chiriquí Lagoon, *Seibert 1650;* Finca 11, west of Almirante, *Stern & Chambers 109;* Water Valley, *von Wedel 593, 843;* Western River, Chiriquí Lagoon, *von Wedel 2705, 2775, 2777;* locality unknown, *Kluge 65, Stern 168.* CANAL ZONE: Fort Sherman, *Allen 118, Standley*

Figure 138. Pterocarpus officinalis Jacq.: A, flowering and fruiting branch (× 1); B, flower (× 5); C, petals (× 4), C[1], vexillum, C[2], wing, C[3], carina; D, androecium and receptacle (× 15); E, pistil (× 5). A after *Stern & Chambers 168* (MO); B-E after *Allen 17154* (MO).

31173; Chiva-Chiva Trail to Searchlight Station, *Hunter & Allen 950;* Barro Colorado Island, *Bangham 502;* south of Salamanca Hydrographic Station, *Steyermark & Allen 17154.* darien: El Real, *Duke 4931;* Punta Guaya Chiquita, *Stern & Chambers 168;* Campamento Buena Vista, Río Chucunaque above Río Tuquesa, *Stern, Chambers, Dwyer & Ebinger 859.* panama: Arraiján, *Allen 2146;* San José Island, *Johnston 789, 790;* Gatuncillo River, *Rowlee & Rowlee 422.*

P. officinalis is a lowland species; the bark is rough and the wood soft and

elaborating a red sap. The wood is useful in various kinds of construction and has the unusual property of being combustible in the fresh state. The flowers are yellow-orange with a red stripe on the vexillum. There are a number of common names: *bloodwood, swamp kaway, sangre, sangre de drago, huevo de gato, cricamola, and chuella.* I. M. Johnston (Sargentia **8:** 160. 1949) states that the fruits are apparently ripe in November and December and are washed up on the beaches (Bodega Bay, San José Island).

7. PLATYMISCIUM Vogel

PLATYMISCIUM Vogel, Linnaea **11:** 198. 1837.

Trees or shrubs. *Leaves* opposite to whorled, the leaflets several, pinnate, opposite, subcoriaceous, pinnately nerved, reticulate; stipules caducous. *Racemes* (or panicles) solitary to several in the axils of the new leaves or arising at exfoliate nodes; bracts and bracteoles minute; pedicels obvious. *Flowers* with the hypanthium campanulate, the teeth 5, short; vexillum orbicular or ovate; wing petals oblong, about equal to the carinal petals in length, unequal at the base; carinal petals oblong, coherent distally; stamens monadelphous, the sheath open or closed above, or occasionally diadelphous, the anthers versatile; ovary stipitate, oblong. *Fruits* indehiscent, flat, membranous, vaguely reticulate, the seeds flat, reniform, large, the rostellum inflexed.

A genus of about 20 species confined to tropical America; only one species is reported from Panama.

1. PLATYMISCIUM POLYSTACHYUM Benth. ex Seem., Bot. Voy. Herald 111, *t. 21.* 1853.—Fig. 139.

Amerimnon pinnatum Jacq., Sel. Stirp. Am. Hist. 200, *t. 47, fig. 50.* 1763.
Platymiscium dubium Pittier, Contr. U. S. Nat. Herb. **20:** 125. 1918.
Platymiscium pinnatum (Jacq.) Dugand, Contr. Hist. Nat. Colomb. **1:** 11. 1938.

Tree. Leaves opposite; leaflets 4-7, opposite, ovate, ovate-rotund, oblong, or elliptic, 5.5-21 cm. long, 4-8 cm. wide, acuminate, often falcately so, or obtuse, occasionally cuneate at the base, occasionally decurrent for 1-3 mm. along the petiolule, chartaceous to thinly coriaceous, the main veins about 10; petioles 0.1-0.6 cm. long, swollen at the base; stipules interpetiolar, triangular-subulate, up to 1.2 cm. long, acute, glabrous, deciduous, the scar distinct. *Inflorescences* either flabellate-paniculate on short, gnarled branches, the rhachis up to 12 cm. long, or in axillary racemes shorter than the leaves; flowers numerous, patulous, often paired in the panicles; pedicels 3-5 mm. long, glabrous; bracteoles ovate. *Flowers* with the hypanthium campanulate, about 4 mm. long, densely puberulent, the teeth unequal, the uppermost pair united along most of their length, the free parts about 0.3 mm. long, subuncinate, the 3 lower teeth 0.7-1.0 mm. long; vexillum orbicular, 6-11.5 mm. long, obtuse at the base, pilulose within; wing petals narrowly oblong, about 10 mm. long; carinal petals subreniform, 8-9.5 mm. long; staminal sheath 5-8 mm. long, open above, 1-1.3 mm. wide, the filaments 2-3.3 mm. long, often farinose at the tips, the anthers 0.6-0.9 mm. long; ovary stipitate for about 5.5 mm., 2-3 mm.

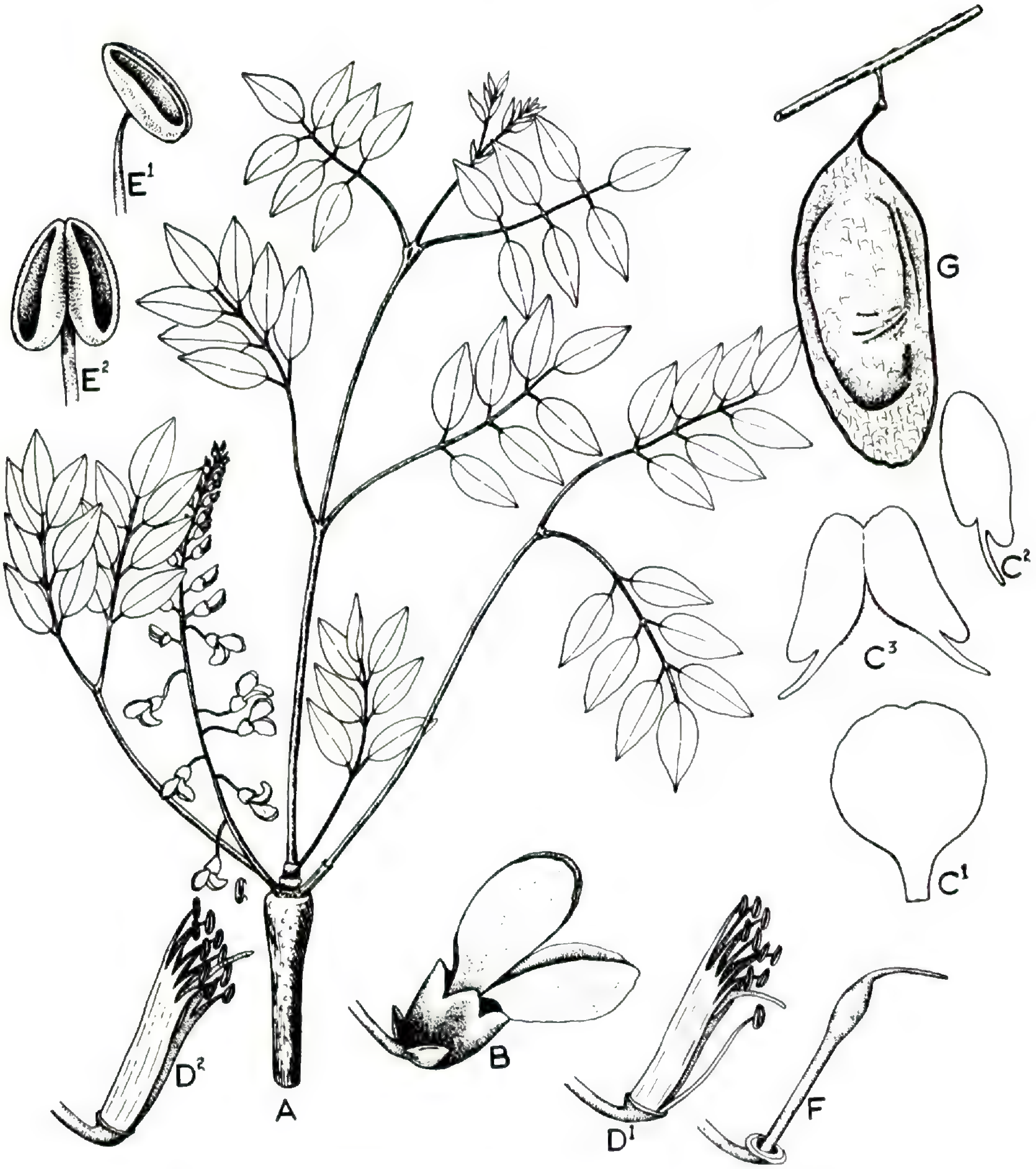

Figure 139. Platymiscium polystachyum Benth.: A, habit (× 1); B, flower (× 5); C, petals (× 4), C[1], vexillum, C[2], wing, C[3], carina; D, androecium (× 5), D[1], diadelphy and pistil in part, D[2], monadelphy; E, anthers (much enlarged), E[1] and E[2], stages of dehiscence; F, pistil (× 7); G, fruit (× 1). A after *Allen 1633* (MO); B-G after *Pittier 5724* (US).

long, glabrous or a with a few, very short hairs, the style 2-2.5 mm. long, glabrous. *Fruit* stipitate for about 1 cm., 5-10 cm. long, obtuse, reticulate, glabrous, apparently often glaucous, the seminiferous area oblong, up to 2 cm. long, the seeds solitary.

Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Trinidad, Colombia, and Venezuela.

CANAL ZONE: Barro Colorado Island, *Carpenter 51;* Hospital Grounds, Ancón, *Pittier 5724.* COCLÉ: Penonomé, *R. S. Williams 395.* DARIEN: Pinogana, *Pittier 6557;* Río Congo, *Pittier 6988.* PANAMA: Río Las Lajas, *Allen 1633;* Chorrera, *Allen 1699.*

The wood is hard and streaked with black and red and is used extensively in furniture and cabinets. According to Seemann the vernacular name is *quira* and the commercial names are *redwood* and *venicola.* The flowers are yellow or orange.

8. PISCIDIA L.

PISCIDIA L., Syst. Nat. ed. 10, 1155. 1759, nom. gen. conserv.

Ichthyomethia P. Browne, Civ. Nat. Hist. Jamaica 296. 1756.

Trees. Leaves imparipinnate, apparently estipulate; leaflets opposite, several. *Panicles* axillary, short; bracteoles elliptic, caducous. *Flowers* with the hypanthium subcampanulate or urceolate, the teeth minute; standard orbicular, the wing petals adhering to the keel petals, the latter obtuse; stamens 10, monadelphous, the vexillar filament free at the base, soon united with the others in a closed sheath; ovary sessile, pluriovulate, the style reflexed, the stigma minute, capitate. *Fruits* slender, the seminiferous area terete, with 4 membranous wings, the seeds several, oblong, black.

A monotypic genus extending from tropical Florida to Venezuela; apparently introduced into Hawaii.

1. PISCIDIA PISCIPULA (L.) Sargent, Garden and Forest **4:** 436. 1891.—Fig. 140.

Erythrina piscipula L., Sp. Pl. 707. 1753.
Piscidia erythrina L., Syst. Nat. ed. 10, 1155. 1759.
Ichthymethia piscipula Hitchcock in Sargent, loc. cit., 472. 1891.

Tree, large. *Leaves* with 6-10 leaflets, obovate-oblong, often inequilateral, up to 9.5 cm. long, up to 5.5 cm. wide, tapering obtusely but shortly acuminate and mucronate at the tip, thinly coriaceous, apparently glabrous above and below, the costa plane above, the main veins 8-11; petioles 1.5-2 cm. long, puberulent; petiolules up to 0.6 cm. long, contorted, minutely puberulent; rachises 4-7 cm. long racemes axillary, up to 13 cm. long, often very nodose above, the branches often several at the base of the rachis, 2-15 cm. long; bracteoles reniform, up to 0.9 cm. long, densely puberulent on the outside. *Flowers* with the calyx campanulate, about 6 mm. long, puberulent, persistent, the teeth short, obtuse to acute, the uppermost usually united; vexillum orbicular, about 12 mm. long, puberulent on the outside; wing petals semiorbicular, about 13 mm. long, glabrous, irregularly undulate on the upper margin, the auricles rounded, about 1.1 mm. long; carinal petals subreniform, about 10.5 mm. long, pubescent; stamens monadelphous, the sheath glabrous, carnose, almost 3 times the length of the filaments, the odd filament free for about 2 mm. at the base; ovary scarcely stipitate, curved, linear, about 1 mm. wide, somewhat flat, densely puberulent, the style thickly subulate, puberulent along ⅔ of its length, attenuate at the tip. *Fruits* pedicellate, the pedicel about 1 cm. long, very slender and puberulent, the body stipitate for 1-1.5 cm. terete, the wings 4, longitudinal, each wing rectangular, 3-7 cm. long, about 4 cm. wide, truncate at the apex and at the base, thinly membranous, the veins crowded, pinnate, glabrous.

Florida, West Indies, Mexico, southward to Venezuela.

CANAL ZONE: Madden Dam, *Allen 4315.*

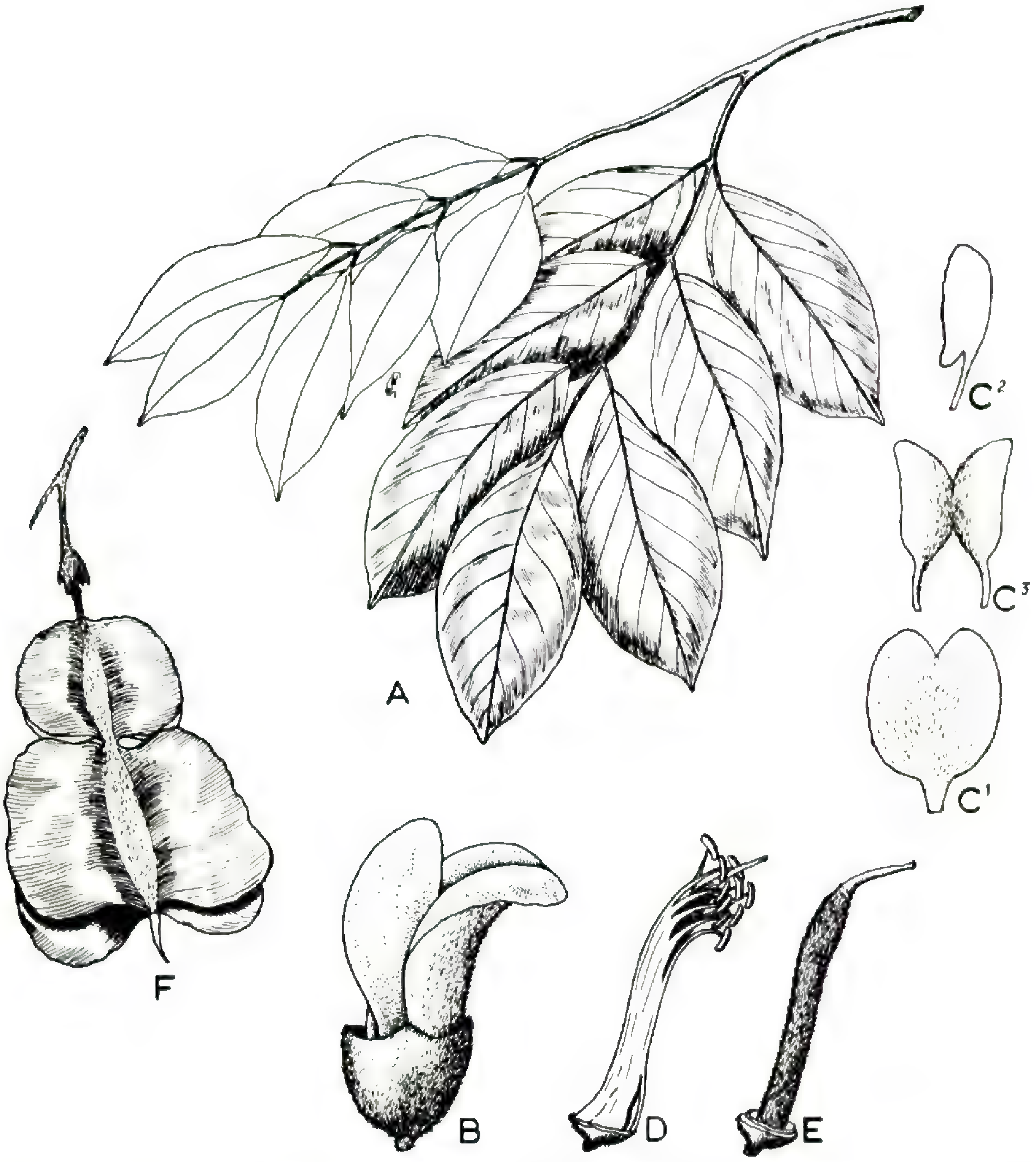

Figure 140. Piscidia piscipula (L.) Sarg.: A, leaves (× 1); B, flower (× 5); C, petals (× 3), C^1, vexillum, C^2, wing, C^3, carina; D, androecium (monadelphy) with part of pistil (× 6); E, pistil (× 6); F, fruit with persistent calyx (× 1). A after *Gentle 1640* (MO); B-F after *Allen 4315* (MO).

P. piscipula is known as the fish poison tree, the extract from the bark being used in stupefying fish. The crystalline salt from the alkaloid is known as piscidin and has remarkable sedative and soporific properties. J. F. Rock (in The Leguminous Plants of Hawaii 171. 1920) discusses the pharmacological properties of *P. piscipula.* The wood is very hard; the flowers are described as pale pink; the fruits with their four conspicuous wings are exceptionally striking.

9. MUELLERA L. f.

Muellera L. f., Suppl. Pl. Syst. Veg. 53. 1781, nom, gen. conserv.

Coublandia Aubl., Hist. Pl. Gui. Fr. 937. 1775.

Trees or shrubs. *Leaves* with several leaflets pinnately disposed; bracts and bracteoles minute, deciduous. *Flowers* with the hypanthium campanulate to cyathi-

form, truncate, the 5 teeth short; vexillum suborbicular, lacking auricles or callosities; wing petals curved, oblong, adhering to the keel petals, the latter oblong; stamens monadelphous, the odd filament free at the base, the anthers versatile; ovary shortly stipitate, without a glandular disk, the style curved, glabrous, the stigma minute. *Fruits* somewhat terete, thick, leathery, indehiscent, sometimes globose or moniliform; seeds numerous, numerous, occasionally solitary, ovoid to subglobose, the hilum lateral, somewhat incurved.

A genus of about three species; apparently rare in Central America, occasional in the West Indies, and apparently well represented in northern South America; only one species is known from Panama.

1. MUELLERA MONILIFORMIS L. f., Suppl. Syst. Veg. 53. 1781.—Fig. 141.

Coronilla monilis L., Pl. Surin. 13. 1775.
Coublandia frutescens Aubl., Hist. Pl. Gui. Fr. 937. 1775.
Lonchocarpus pterocarpus DC., Prodr. **2**: 260. 1825.
Sphinctolobium glaucescens Miq., Stirp. Surin. Sel. 19, *t. 4.* 1850.
Derris moniliformis (L. f.) Ducke, Bol. Téc. Inst. Agron. Norte (Belém) **2**: 29. 1944.

Tree up to 35 m. high. *Leaves* with (3-)5-7 leaflets, these elliptic, 6-17 cm. long, 4-9 cm. wide, acute or with an acumen up to 2 cm. long, obtuse at the base, stiffly chartaceous, bicolor, gray beneath, often reticulate, glabrous above, minutely puberulent beneath, the costa plane or subimmersed above, the main veins 6-10, arcuate; petioles 5-6 cm. long; rachises 3-6 cm. long, stiff, glabrous, apparently angular; petioles about 0.5 cm. long, stiff and at right angles to the petioles, densely puberulent. *Panicles* with rachises up to 7.5 cm. long, puberulent, the flowers few, patulous; pedicels about 8 mm. long, glabrous. *Flowers* with the hypanthium galeate, bowl-shaped, 3-6 mm. long, thinly carnose, minutely puberulent, the teeth absent or minute, deltoid to mammiform, 0.5-2.5 mm. long; vexillum reflexed, oblong-rotund, 12-30 mm. long, 9-13 mm. wide, occasionally aurous-puberulent at the apex, the auricles not evident, the claw thickened, 2-10 mm. long, glabrous; wing petals narrowly ovate-oblong, 12-18 mm. long, often puberulent at the tip, the claw about 4 mm. long; carinal petals oblong-subreniform, 11-15 mm. long, the margin at the apex thickened, velutinous, the claw 3-5 mm. long; staminal sheath flat, about 6 mm. long, geniculate at the base, the filaments thickened, the anthers about 0.8 mm. long, apiculate, often with a few hairs, the odd filament free at the base, then briefly united to the sheath, the latter closed at the base; ovary sessile, flat, subsigmoid, 5-7 mm. long, villose, the style thickly subulate, 4-7 mm. long, about 0.6 mm. wide, glabrous. *Fruits* pedicellate for about 0.3 cm., rotund or nuciform, occasionally oblong, 2.5-5 cm. long, often constricted 1 to 3 times, the pericarp corky, the seeds 1-4, flat, suborbicular, about 1.5 cm. long.

Panama, Trinidad, and continental northern South America.

BOCAS DEL TORO: Chiriquí Lagoon, Fish Creek Hills, *von Wedel 2452.* CANAL ZONE: Experimental Garden, Old Plot #4, *Higgins 498.* DARIEN: Río Congo, *Pittier 6893;* Puerto St. Dorotea, *Dwyer 2291.*

The species is readily recognized by the stiff rachises and petiolules, the fili-

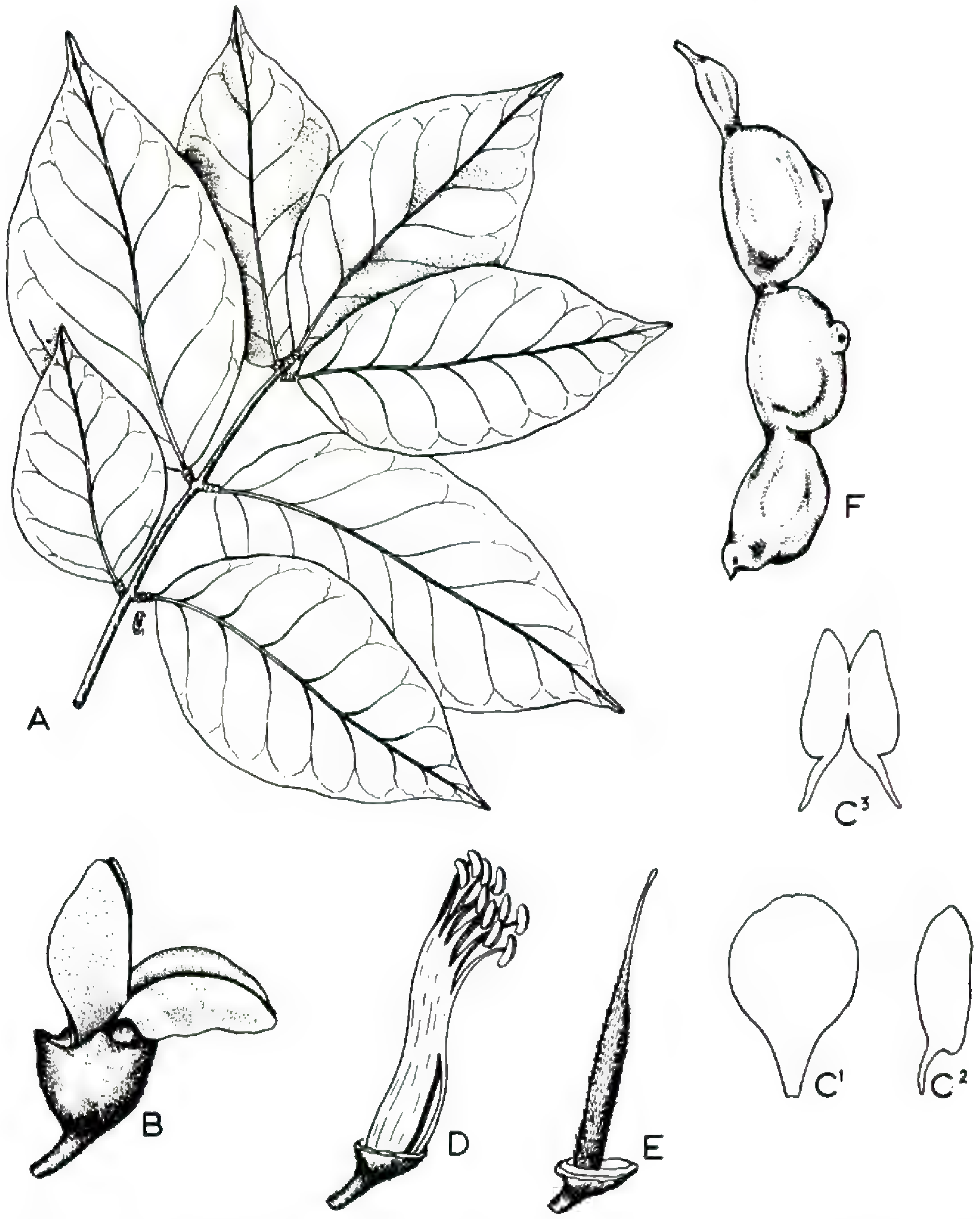

Figure 141. Muellera moniliformis L. f.: A, leaf (× 1); B, flower (× 4); C, petals (× 3), C[1], vexillum, C[2], wing, C[3], carina; D, androecium (monadelphy) (× 6); E, pistil (× 8); F, fruit (× 2). A-E after *von Wedel 2442* (MO); F after *Dwyer 2291* (MO).

form pedicels of the flowers and the fruits which are usually moniliform. The flowers are purple. Macbride's remark (Field Mus. Nat. Hist., Bot. Ser. **13**(3): 258. 1943) that in *Muellera* ". . . one species . . . is one-seeded . . . and in the other more common one . . . is . . . usually several to many seeded . . ." is confusing since the well-known *M. moniliformis* (to which Macbride is obviously referring in the latter part of his statement) is known to vary greatly in the morphology of the fruits and in the number of seeds contained. Amshoff (in Pulle, Fl. Suriname **2**(2): 148. 1939) states that the leaflets are pellucid-punctate. I have not been able to verify this in dried material.

10. LONCHOCARPUS H. B. K.

BY F. J. HERMANN

LONCHOCARPUS H. B. K., Nov. Gen. Sp. Pl. **6:** 383. 1824, nom. gen. conserv.

Clompanus Aubl., Hist. Pl. Gui. Fr. 773. 1775.

Trees or shrubs. *Leaves* alternate, odd-pinnate (rarely 1-foliolate); leaflets opposite, mostly estipellate. *Flowers* purple, pink or whitish, borne in paniculate racemes; pedicels geminate or fasciculate on generally rudimentary secondary peduncles, rarely solitary or racemose; bracts and bractlets generally small, caducous or persistent; calyx mostly cupulate, truncate or minutely toothed; vexillum usually orbicular, generally auriculate at the base, emarginate at the apex; wing petals oblique-oblong or falcate, adhering to the carinal petals above the claw; carinal petals obtuse, more or less arcuate, connate along their lower margin; stamens monadelphous, the tube fenestrate at the base; vexillar stamen free at the base; anthers versatile; ovary sessile or stipitate, 2- to 10-ovulate; style filiform, arcuate; stigma capitellate. *Legumes* indehiscent, oblong or suborbicular to elongate, flat, membranous or coriaceous, the vexillar suture thin, concave, thickened or carinate; seeds 1-4, compressed, more or less reniform.

About 175 species in Central and South America, West Indies, Africa and Australia; 13 species and two varieties are presently reported from Panama. The South American *L. nicou* (Aubl.) DC. is now the principal source of *rotenone.*

a. Flowers in pairs on short, secondary peduncles racemosely arranged along the floral axis.
  b. Vexillar margin of the legume sharp-edged or rounded.
    c. Midrib and secondary veins impressed on the upper surface of the leaflets, very prominent beneath; legume pubescent.
      d. Legume coriaceous, elliptic, 2.5 cm. wide, appressed-sericeous; flowers pinkish-purple, the wing petals subfalcate, 13.5 mm. long, 3.5 mm. wide; leaflets 7-13 .... 1. L. FENDLERI
      dd. Legume submembranous, elongate to linear-lanceolate, 1.5-1.7 cm. wide, velutinous; flowers deep-purple, the wing petals narrowly oblong, 8 mm. long, 2 mm. wide; leaflets 7 (rarely 5 or 9) .... 2. L. VELUTINUS
    cc. Midrib and secondary veins not conspicuously impressed on the upper surafce of the leaflets; legume glabrous.
      d. Leaflets pellucid-punctate.
        e. Leaflets 2.5-4.5 cm. wide, abruptly accuminate to caudate at the apex; legume oblique-ovate to ovate-lanceolate, 4.5-6.5 cm. long (when rarely 3-seeded up to 13 cm. long), coriaceous, substipitate .... 3. L. PENINSULARIS
        ee. Leaflets 4.5-6 cm. wide, subacuminate to an obtuse apex; legume broadly oblong, 10 cm. long, subligneous, long-stipitate .... 4. L. CHIRICANUS
      dd. Leaflets epunctate.
        e. Legume orbicular to oblong, rounded or abruptly acute at base and apex; vexillum 10-12 mm. long; racemes generally compound or apparently fastigate and terminal .... 5. L. LUTEOMACULATUS
        ee. Legume elliptic, cuneate-attenuate at base and apex; vexillum 5-7 mm. long; racemes generally simple, axillary .... 6. P. PENTAPHYLLUS
  bb. Vexillar margin of the legume thickened at the seeds, carinate or concave.
    c. Leaves 1-foliolate .... 7. L. MONOFOLIARIS

cc. Leaves multifoliolate.
d. Vexillum about 9 mm. long, the margins strongly inflexed.
e. Leaflets 2-6.5 cm. long, 1-3 cm. wide; petiolules 2-3 mm. long; secondary peduncles predominantly biflorous, 2-3 mm. long; vexillum sparsely sericeous toward the apex outside, its claw 0.8 mm. long .... 8. L. ATROPURPUREUS
ee. Leaflets 6-15 cm. long, 2.5-7 cm. wide; petiolules 4.5-6 mm. long; secondary peduncles uniflorous, 0.5 mm. long; densely sericeous outside, its claw 1.5 mm. long .... 9. L. OLIGANTHUS
dd. Vexillum 12-16 mm. long, the margins not inflexed.
e. Leaflets pellucid-punctate; petiolules glabrous.
f. Flowers 10-13 mm. long; calyx in anthesis generally 6 mm. wide or less, usually densely sericeous; rachis of inflorescence densely canescent; secondary peduncles usually 0.5-1 mm. long .... 10. L. GUATEMALENSIS
ff. Flowers 13-16 mm. long; calyx in anthesis generally 7 mm. wide or more, usually sparsely sericeous; rachis of inflorescence glabrous; secondary peduncles usually 2-2.5 mm. long .... 10a. —var. PROTERANTHUS
ee. Leaflets epunctate; petiolules pubescent.
f. Leaflets scabridulous-puberulent above, tomentulose to densely puberulent beneath .... 11. L. SERICEUS
ff. Leaflets glabrous above, glabrate or minutely puberulent (principally on the veins) beneath .... 11a. —var. GLABRESCENS
aa. Flowers not paired, in short racemes (or by abortion subfasciculate) arranged along the floral axis.
b. Secondary inflorescences racemose; leaflets estipellate .... 12. L. CALCARATUS
bb. Secondary inflorescences subfasciculate; leaflets stipellate .... 13. L. DENSIFLORUS

1. LONCHOCARPUS FENDLERI Benth., Jour. Linn. Soc., Bot. **4** (Suppl.): 94. 1860.

Lonchocarpus stenurus Pittier, Bol. Minist. Relac. Exter. Venez. **8-9**: 102. 1927.

Tree 4-12 m. high. *Leaves* 7- to 13-foliolate, appearing with the flowers; leaflets ovate-oblong or slightly obovate, 3-9 cm. long, 2-4 cm. wide, rounded or tapering at the base, obtuse or subacute at the apex, at length coriaceous, glabrous and often lustrous above, more or less rufous-tomentose beneath. *Racemes* axillary, 10-14 cm. long. *Flowers* with the calyx turbinate-campanulate 5 mm. long, cinereous-strigose, the teeth obsolete; petals pinkish-purple; vexillum orbicular, 11-12 mm. long, attenuate at the base, sparsely pubescent within; wing petals oblong, subfalcate, auriculate, the claw 5 mm. long, the blade about 9 mm. long, glabrous or sparsely pilulose without; staminal tube narrowly fenestrate; anthers sparsely setulous at the base. *Legumes* subsessile or short-stipitate, flattened, elliptic, about 8 cm. long, 2.5 cm. wide, coriaceous, 1 (rarely 2-4)-seeded, appressed-sericeous.

Panama and Venezuela; not previously reported from Central America.

BOCAS DEL TORO: Island Potrero, Changuinola Valley, *Dunlap* 347.

2. LONCHOCARPUS VELUTINUS Benth. ex Seem., Bot. Voy. Herald 111. 1853.

Tree 5-16 m. high. *Leaves* predominantly 7 (rarely 5-or 9-)-foliolate; leaflets oval or oblong, 4-15 cm. long, 2-5 cm. wire, acute at the base, short-acuminate to obtuse or retuse at the apex, velutinous. *Racemes* axillary, 11-20 cm. long; bractlets

linear, caducous, distant from the calyx. *Flowers* with the calyx salverform, 5-dentate; petals dark purplish-red; vexillum orbicular, 9 mm. long, minutely sericeous within; wing petals narrowly oblong, the claw about 2.5 mm. wide, the blade 5.5 mm. long; anthers sparsely and minutely hairy. *Legumes* thin and flattish, elongate- to linear-lanceolate, 8-11 cm. long, 1.5-1.7 cm. wide, submembranous, stramineous or pale yellow, 1- or 2-seeded.

Central America and Colombia.

CANAL ZONE: Barro Colorado Island, *Shattuck s.n., Woodworth & Vestal 712;* near Miraflores, *P. White 80.* CHIRIQUÍ: around Caldera, alt. 200-300 m. *Pittier* 3353. COCLÉ: Penonomé, *R. S. Williams 349.* VERAGUAS: vicinity of Santa Fé, 1000 ft. alt., *Allen 4439.*

The two collections cited by Seemann in his original description came from Panama; San Carlos, Prov. of Panama, *Seemann 1138,* and Culebra, Canal Zone, *Hinds s. n.*

3. LONCHOCARPUS PENINSULARIS (J. D. Sm.) Pittier, Contr. U. S. Nat. Herb. **20:** 56, *pl. 2, A, fig. 4.* 1917.

Derris peninsularis J. D. Sm., Bot. Gaz. **44:** 111. 1907.
Derris nicoyensis J. D. Sm., loc. cit. 111. 1907.
Lonchocarpus nicoyensis (J. D. Sm.) Pittier, loc. cit. 57, *pl. 2, B, fig. 5.* 1917.
Lonchocarpus cochleatus Pittier, loc. cit. 68, *pl. 4, C.* 1917.
Lonchocarpus purpusii Brandegee, Univ. Calif. Publ. Bot. **6:** 500. 1919.
Lonchocarpus kerberi Harms, Repert. Sp. Nov. **17:** 322. 1921.
Lonchocarpus chiapensis Lundell, Wrightia **1:** 152. 1946.
Lonchocarpus nicaraguensis Lundell, loc. cit. 154. 1946.

Shrub or small tree. *Leaves* 5- to 9-foliolate; leaflets ovate, elliptic or obovate, 4-10 cm. long, 2.5-4.5 cm. wide, acute at the base, abruptly acuminate to caudate at the apex, pellucid-punctate, glabrous above, minutely grayish-strigose beneath. *Racemes* axillary, 6-8 cm. long. *Flowers* with the calyx cupulate, 3-5 mm. long, glabrous or minutely puberulent; petals pink to dark red; vexillum suborbicular, 10 mm. long, more or less cinereous to sericeous outside especially along the veins, the margins inflexed except toward the base; wing petals oblong to somewhat falcate, the claw 2.5 mm. long, the blade 7 mm. long, glabrous. *Legumes* flattened, obliquely ovate to ovate-lanceolate, 4.5-6.5 cm. long (when, rarely, 3-seeded up to 13 cm. long), coriaceous, glabrous, chiefly 1-seeded.

Mexico (Jalisco, Guerreo and Veracruz) to Panama.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1180.*

4. LONCHOCARPUS CHIRICANUS Pittier, Contr. U. S. Nat. Herb. **20:** 63, *pl.* 3, *A.* 1917.

Tree, small. *Leaves* 7- to 9-foliolate; leaflets ovate to obovate, 6-11 cm. long, 4.5-6 cm. wide, rounded at the base, abruptly acuminate to a short, blunt apex, membranous, dark green and glabrous above, paler and minutely pilosulous beneath, pellucid-punctate. *Flowers* unknown. *Legumes* long-stipitate, flattened, broadly oblong, 10 cm. long, 4 cm. wide, subligneous, glabrous, 1-seeded.

Panama; known only from the type collection.

CHIRIQUÍ: Parida Island, *Pittier 2817* (type).

5. LONCHOCARPUS LUTEOMACULATUS Pittier, Contr. U. S. Nat. Herb. **20:** 64, *pl. 4, B, fig. 12.* 1917.

Lonchocarpus izabalanus Blake, Contr. U. S. Nat. Herb. **24:** 7. 1922.
Lonchocarpus monospermus Standley, Field Mus. Nat. Hist., Bot. Ser. **4:** 311. 1929.
Lonchocarpus belizensis Lundell, Wrightia **1:** 55. 1945.

Tree 4.5-9 m. high. *Leaves* 5- to 9-foliolate; leaflets elliptic-ovate or obovate to oblanceolate-oblong, 6-14 cm. long, 3-7 cm. wide, rounded to cuneate at the base, subacuminate to rounded at the apex, membranous to subcoriaceous, finely strigillose, dark green above, glaucescent beneath. *Racemes* mostly compound, axillary or subfasciculate, sometimes appearing terminal, 9-15 cm. long. *Flowers* with the calyx cupulate, 3 mm. long, rusty-strigillose, the depressed-deltoid teeth acutish, the lower one longer and acute; petals dark red or maroon; vexillum suborbicular, 10-12 mm. long, yellow or greenish centered, densely silky-strigillose outside with reddish hairs; wing petals oblique-oblong, the claw 2-2.5 mm. long, the blade 7-9 mm. long, slightly strigillose near the base. *Legumes* short-stipitate, strongly compressed, orbicular to broadly ovate-elliptic or oblong, 2.5-4.5 cm. long, 1.5-2.2 cm. wide, rounded or abruptly acute at base and apex, coriaceous, minutely appressed-pilose, ochraceous, 1- or 2-seeded.

British Honduras, Guatemala, Honduras, and Panama.

BOCAS DEL TORO: vicinity of Almirante, *Cooper 549.* CANAL ZONE: near Fort Sherman, *Bailey & Bailey 213.* COLÓN: *Chagres, Fendler 94;* along Río Santa Isabel, *Pittier 4170.*

6. LONCHOCARPUS PENTAPHYLLUS (Poir.) DC. Prodr. **2:** 259. 1825.—Fig. 142.

Dalbergia pentaphylla Poir. in Lam., Encyd. Méth. Bot. Suppl. **2:** 445. 1812.
Lonchocarpus latifolius DC., Prodr. **2:** 260. 1825, non *Amerimnum latifolium* Willd. in L., Sp. Pl. ed. 4 [i.e. 5], **3:** 909. 1802.

Tree 10-15 m. high. *Leaves* 5- to 9-foliolate; leaflets usually large, ovate to elliptic-oblong, 7-24 cm. long, 4-12 cm. wide, from acuminate to rounded at the base, short-acuminate to subobtuse at the apex, membranous to subcoriaceous, dark green to almost glabrous above, paler and minutely strigillose beneath. *Racemes* solitary in the upper leaf-axils, 5-12 cm. long. *Flowers* with the calyx broadly cupulate, 3 mm. long, minutely but densely sericeous, 5-dentate; petals purplish-red or greenish-purple; vexillum orbicular, truncate at the base, 5-7 mm. long, often yellow-centered, densely tawny silky-strigillose outside; wing petals oblong, short-auriculate, the claw 2.3 mm. long, the blade 5.5 mm. long, sparsely strigillose outside. *Legumes* strongly compressed, elliptic, 4.5-6.5 cm. long, 1.8-2.5 cm. wide, cuneate-attenuate at both ends, submembranous, very minutely sericeous to glabrate.

West Indies, Central and northern South America.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 141;* Isla Colón, *von Wedel 100;* Fish Creek Hills, vicinity of Chiriquí Lagoon, *von Wedel 2447.* CANAL ZONE: Barro Colorado Island, *Brown 124.* COCLÉ: Bismark above Penonomé, *R. S. Williams 317.* COLÓN: Portobelo, *Dwyer 5001,* Río Indio de Fató, *Pittier 4269.* PANAMA: San José Island, *Erlanson 57, Johnston 1563.* SAN BLAS: Permé, *Cooper 225, 227.* VERAGUAS: Isla De Coiba, *Dwyer 1561.*

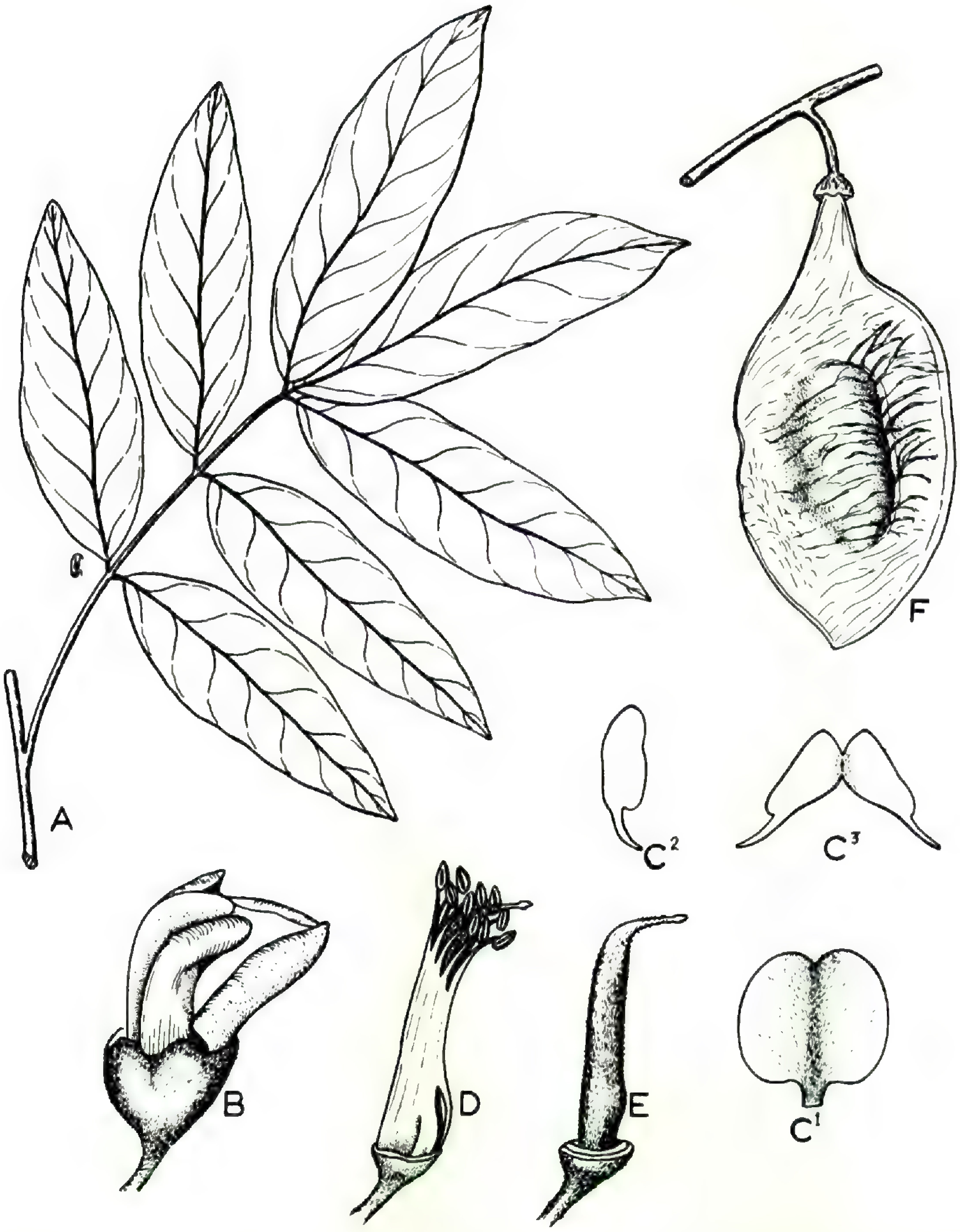

Figure 142. LONCHOCARPUS PENTAPHYLLUS (Poir.) DC.: A, leaf (× 1); B, flower (× 7); C, petals (× 4), C[1], vexillum, C[2], wing, C[3], carina; D, androecium (monadelphy) (× 8); E, pistil (× 8); F, fruit showing seed in outline (× 1). A-E after *Johnston 1563* (MO); F after *Dwyer 1561* (MO).

As noted by C. O. Erlanson on the label of his collection and by I. M. Johnston (Sargentia **8:** 154. 1949), the species is markedly myrmecophilous. Johnston points out (loc. cit.) that the dubious name *L. latifolius* should be displaced by the well-founded *L. pentaphyllus*.

7. LONCHOCARPUS MONOFOLIARIS Schery, Ann. Missouri Bot. Gard. **30:** 89. 1943.

Tree 5-13 m. high. *Leaves* 1-foliolate; petioles 8-9 mm. long; leaflets oblong-to oval-elliptic, 14-18 cm. long, 5.5-8 cm. wide, acute to subobtuse at the base, caudate to a narrow blunt apex, subcoriaceous, glabrous, with about 12 prominent

arcuate lateral veins beneath; petiolules 2-3 mm. long. *Flowers* with the calyx very shallowly cupulate to salverform, very shallowly dentate (except for the prominent lowermost tooth), 1.5 mm. long, strigillose; petals lilac to violet-blue; vexillum orbicular, subauriculate at the base, retuse and inflexed at the apex, 8-9.5 mm. long, sericeous without; wing petals narrowly oblong, subfalcate, conspicuously auriculate, the claw 3 mm. long, the blade 7 mm. long, with a broad, sericeous, median band without. *Legumes* stipitate, thin, compressed, broadly oblique-elliptic, 5-7 cm. long and 2.5-3 cm. wide (when 1-seeded), to oblong, 7-8.5 cm. long and 2.5 cm. wide (when 2-seeded), generally abruptly attentuate at both ends, subcoriaceous, pale green, glabrous or very sparsely strigose, prominently veined, the upper margin somewhat thickened and distinctly concave above the seeds.

Costa Rica and Panama.

BOCAS DEL TORO: Water Valley, *von Wedel 699* (type), *910, 1502;* vicinity of Chiriquí Lagoon, *von Wedel 1027, 1603.*

8. LONCHOCARPUS ATROPURPUREUS Benth., Jour. Proc. Linn. Soc., Bot. **4** (Suppl.): 91. 1860.

Shrub or tree 3-15 m. high. *Leaves* 5- to 9-foliolate; leaflets ovate-oblong to lanceolate, 2-6.5 cm. long, 1-3 cm. wide, obtuse to cuneate at the base, acuminate to an obtuse apex, subcoriaceous, dark green and glabrous above, paler and puberulent or sericeous beneath. *Racemes* slender, axillary, 1.5-8 cm. long. *Flowers* with the calyx broadly cupulate, 2 mm. long, minutely pubescent, at maturity subentire; petals dark purple or pinkish-purple; vexillum suborbicular, 9 mm. long, the lateral margins inflexed, deeply emarginate and slightly pubescent outside at the apex, otherwise glabrous; wing petals oblong, auriculate, the claw 2.2 mm. long, the blade 7.5 mm. long, glabrous. *Legumes* long-stipitate, compressed, flat, linear-oblong, 4-10 cm. long, 1 cm. wide, obtuse at the apex, glabrous, 1- to 4-seeded.

Southern Mexico, Guatemala, Honduras, Costa Rica, Panama, Venezuela, and Ecuador.

CANAL ZONE: vicinity of Madden Dam, *Allen 2012, Stern & Chambers 160.* COLÓN: Río Gatuncillo, vicinity of Santa Rosa, *Allen 4162.*

9. LONCHOCARPUS OLIGANTHUS Hermann, Ann. Missouri Bot. Gard. **36:** 281. 1949.

Shrub or slender tree about 10 m. high. *Leaves* 5- to 7-foliolate; leaflets oblong to elliptic, 6-15 cm. long, 2.5-7 cm. wide, rounded or tapering at the base, caudate at the apex, thin-chartaceous, copiously strigose when young, at maturity glabrous or minutely and sparingly strigose beneath, multi-punctate. *Racemes* axillary, slender, subspiciform, loosely flowered, 6-10 cm. long. *Flowers* with the calyx cupuliform, 2.5-3 mm. long, minutely tawny-strigose, the teeth (except the broadly deltoid, carinal tooth) obsolete; petals purple; vexillum broadly oblong to oblong-obovate, 9 mm. long, reflexed, deeply emarginate and somewhat cucullate at the apex, the lateral margins strongly inflexed, copiously silvery-sericeous without; wing petals

oblong, shallowly auriculate, the claw 2.5 mm. long, the blade 6.5 mm. long, glabrous except for a sericeous, median band. *Legumes* unknown.

Costa Rica and Panama.

BOCAS DEL TORO: Garay Creek, vicinity of Chiriquí Lagoon, *von Wedel 2634* (type).

10. LONCHOCARPUS GUATEMALENSIS Benth., Jour. Proc. Linn. Soc., Bot. **4** (Suppl.): 87. 1860.

Lonchocarpus darienensis Pittier, Contr. U. S. Nat. Herb. **20**: 69, *fig. 18.* 1917.
Lonchocarpus dumetorum Brandegee, Univ. Calif. Publ. Bot. **10**: 181. 1922.

Tree 3-20 m. high. *Leaves* 5- to 9-foliolate; leaflets elliptic to oblong or ovate, 3.5-11 cm. long, 2-5 cm. wide, subcuneate to rounded at the base, abruptly acuminate to an obtuse apex, subcoriaceous, pellucid-punctate, glabrous. *Racemes* axillary, solitary or fasciculate, 3-14 cm. long. *Flowers* appearing with or before the new leaves; calyx cupulate, 4.5-5.5 mm. long, gray-sericeous; petals pale lavender shading to white toward the claw; vexillum suborbicular, 10-13 mm. long, more or less truncate at the base, emarginate at the apex, sericeous without; wing petals oblong, prominently auriculate, the claw 4.5-5 mm. long, the blade 8 mm. long. *Legumes* stipitate, thin, flat, 7-12 cm. long, 1.5-3 cm. wide, 1- to 3-seeded, narrowed at both ends, glabrous, pale brown, the upper margin dilated and deeply sulcate between the valve-margins.

Mexico (Sinaloa) to Panama.

DARIEN: in forest near sea level around Garchine, *Pittier 5515* (type of *L. darienensis*).

10a. LONCHOCARPUS GUATEMALENSIS var. PROTERANTHUS (Pittier) Hermann, Jour. Wash. Acad. Sci. **39**: 312. 1949.

Lonchocarpus proteranthus Pittier, Contr. U. S. Nat. Herb. **20**: 63, *pl.* 3, *B*, *fig. 11.* 1917.

Differing from the typical form in its somewhat larger flowers (13-16 mm. rather than 10-13 mm. long), sparsely sericeous and wider calyx (7 mm. rather than 6 mm. or less), glabrous inflorescence-rachis, and longer secondary peduncles (2-2.5 mm. rather than 0.5-1 mm. long).

Known only from Panama.

COCLÉ: Penonomé and vicinity, *R. S. Williams 418* (type).

11. LONCHOCARPUS SERICEUS (Poir.) DC., Prodr. **2**: 260. 1825.

Robinia sericea Poir. in Lam., Encycl. Méth. Bot. **6**: 226. 1804.
Lonchocarpus pyxidarius DC. loc. cit. 260. 1825.
Lonchocarpus cruentus Lundell, Wrightia **1**: 55. 1945.

Tree averaging 10-15 m. in height. *Leaves* 7- to 13-foliolate; leaflets oblong to ovate or obovate, 3-9 cm. long, 2-3.5 cm. wide, rounded at the base, rounded-obtuse or abruptly acuminate to an obtuse apex, coriaceous, minutely pubescent beneath, at least on the midrib and veins. *Racemes* solitary in the upper leaf axils, the rachis

at first velutinous. *Flowers* with large and semipersistent bractlets; calyx cupulate, mostly 4 mm. long, subentire or very shallowly denticulate, densely ferruginous-pubescent; petals rose-pink; vexillum suborbicular, 14-15 mm. long, auriculate at the base, densely silvery-sericeous without; wing petals broadly oblong, very shallowly auriculate, the claw 4.5 mm. long, the blade 10 mm. long, somewhat sericeous without; carina densely sericeous toward the apex; filaments and anthers more or less setose. *Legumes* compressed but thick, 5-12 cm. long, 2.3 cm. wide, somewhat constricted between the seeds, more or less fulvous-pubescent, the vexillar margin carinate and much thickened opposite the 1-5 seeds.

Mexico, Central America, West Indies, northern South America and western tropical Africa.

HERRERA: Santa Maria, *Allen 791*. VERAGUAS: Isla de Coiba, *Dwyer 1713*.

11a. Lonchocarpus sericeus var. glabrescens Benth., Jour. Proc. Linn. Soc., Bot. **4**(Suppl.): 88. 1860.

Lonchocarpus domingensis DC., Prodr. **2**: 259. 1825.
Lonchocarpus lucidus Pittier, Contr. U. S. Nat. Herb. **20**: 77, *fig. 27*. 1917.

Although *L. lucidus* was set off from *L. sericeus* principally on the basis of the lack of a carina on the upper margin of the legumes in the one known fruiting collection, the pods so described are not fully mature and some show a decided tendency toward the development of a carina. The petiolules, moreover, are copiously pubescent, a characteristic of Pittier's section *Carinati* rather than the section *Concavi*. As Bentham pointed out, the least variable characteristic differentiating the plant from *L. sericeus* appears to be the glabrate foliage.

Central America, West Indies, northern South America and western tropical Africa.

COLÓN: along Río Fató, *Pittier 3879*. CANAL ZONE: lake shore along Gatun River Valley, *Pittier 6508*. PANAMA: river valleys near Chepó, *Kluge 22*. DARIEN: Río Chico, vicinity of Yaviza, *Allen 5089*.

12. Lonchocarpus calcaratus Hermann, Ann. Missouri Bot. Garden **36**: 282. 1949.

Tree 9 m. high. *Leaves* 9- to 11-foliolate; leaflets elliptic-lanceolate, 3.5-11 cm. long, 2-4 cm. wide, cuneate or abruptly acute at the base, obtuse at the apex, epunctate, subcoriaceous, the margin indurated, glabrate above, strigose beneath. *Inflorescences* lateral, paniculate, 25 cm. long, the rachis stout, angular, the flowers in short secondary racemes. *Flowers* with the calyx broadly cupulate, 3.5-4 mm. long, densely sericeous-strigose, the margin subentire in anthesis except for the apiculate 2 lower teeth; petals 16-17 mm. long, pink; vexillum orbicular, 15 mm. long, truncate to shallowly cordate at the base, very sparingly sericeous outside the emarginate apex; wing petals cymbiform, the claw 4.5 mm. long, the blade 11.5 mm. long, very sparsely sericeous without; carinal petals calcarate above the claw. *Legumes* unknown.

Known only from Panama.

COCLÉ: El Vallé, *Allen 4472* (type).

13. LONCHOCARPUS DENSIFLORUS Benth., Ann. Nat. Hist. **3:** 433. 1839.

Climbing shrub or small tree. *Leaves* 7- to 11-foliolate; leaflets ovate to oblong-elliptic, 3-8 cm. long, 2-4 cm. wide, rounded or obtuse at the base, abruptly acuminate, subcoriaceous, dark green and glabrous above, paler and strigillose beneath, the petiolules with filiform stipels at their base. *Racemes* axillary, scarcely longer than the leaves, the rachis stout, terete, the flowers fasciculate. *Flowers* with the calyx cupulate, 4-5 mm. long, shallowly denticulate, densely sordid-strigillose; petals purple to blue; vexillum orbicular, 15 mm. long, cordate at base, the apex slightly emarginate, densely strigillose without; wing petals falcate, auriculate at base; carina strongly arcuate, strigillose along the lower margin. *Legumes* flat, the vexillar suture narrowly carinate.

Panama and British Guiana.

BOCAS DEL TORO: Chiriquí Lagoon: *Hart 99, von Wedel 1405;* Almirante, *Rowlee & Stork 1002.* CANAL ZONE: vicinity of Mindi, *Allen 5119.*

11. FISSICALYX Benth.

FISSICALYX Benth., Jour. Proc. Linn. Soc., Bot. **5:** 79. 1861.

Trees, unarmed. *Leaves* alternate, imparipinnate, stipulate. *Inflorescences* paniculate, the ultimate branches racemose; pedicels geniculate. *Flowers* with the hypanthium narrow at the base, oblique and cleft on the lower side toward the apex and thus spathaceous, the teeth obsolete; petals free; stamens 10, monadelphous, the sheath cleft above, the filaments short, the anthers monomorphic, dehiscing at first by 2 apical pores; ovary slender, flask-shaped, with 2 basal ovules, the style slender, the stigma minute. *Fruits* bearing broad, lateral wings, 1-seeded.

A monotypic genus known only from Panama and northern South America.

1. FISSICALYX FENDLERI Benth., Jour. Proc. Linn. Soc., Bot. **5:** 79. 1861.—Fig. 143.

Tree, small to large, the branchlets puberulent. *Leaves* apparently emerging after the flowers, the leaflets 4-14, usually 9 and opposite, ovate (basal pairs) to elliptic-lanceolate (distal pairs), about 8 cm. long, about 3 cm. wide, membranous, reticulate, glabrescent (except the obviously pubescent costa and margins); petioles 2-10 cm. long; rachises about 15 cm. long, pubescent; stipules lanceolate, often acuminate, the acumen up to 1.5 cm. long. *Panicles* terminal, the branches slender, racemose, the pedicels about 6 mm. long, hirsute; bracteoles proximal to the calyx. *Flowers* with the hypanthium inequilaterally fusiform in the bud, later tubular, the limb elliptic, spathaceous, about 10 mm. long, hirsute; vexillum orbicular, about 12 mm. long, complicate, briefly unguiculate, somewhat arachnoid-villose near the tips; stamens with the sheath about 9 mm. long, the filaments up to 2 mm. long, the anthers oblong, 1-1.3 mm. long, dehiscing by paired, terminal pores later extending to lateral slits; ovary stipitate for about 2 mm., narrowly oblong, about 4 mm. long, densely pubescent, the style about 10 mm. long. *Fruits* flat, subrotund,

Figure 143. Fissicalyx fendleri Benth.: A, leaf and inflorescence (× 1); B, fruit showing seed in outline (× 1). After *Allen 4274* (MO).

5-6 cm. long, 4-5 cm. wide, tapering gradually and ultimately truncate and often retuse at the tip, the wings lightly pubescent; seeds about 1.7 cm. long, reddish-brown.

Known from Panama, the Guianas, and Venezuela.

CANAL ZONE: Gamboa, *Allen 4274;* Summit Road, *Jones 271.*

A rather striking tree with orange-yellow flowers, evidently flowering at the end of the dry season in Panama (March). The two collections cited above probably represent the first report of the species in Central America. The spathaceous calyx is not found in any other species of the Panamanian *Dalbergieae* and the poricidally dehiscent anthers are probably unique for the *Papilionoideae.*

12. GEOFFROEA Jacq.

GEOFFROEA Jacq., Sel. Stirp. Am. Hist. 207. July, 1763.

Geoffraea L., Sp. Pl. ed. 2, 1043. August, 1763.
Vouacapoua Aubl., Hist. Pl. Gui. Fr., Suppl. 9, *t. 373.* 1775.
Andira A. L. Jussieu, Gen. Pl. 363. 1789.

Trees, small or large. *Leaves* with 7-15 leaflets pinnately disposed; stippelles linear or subulate, deciduous; stipules small, subulate, caducous. *Panicles* or racemes terminal; bracts and bracteoles small, soon deciduous. *Flowers* with the vexillum mostly suborbicular, auriculate at the base, the claw abrupt, short; wing and carinal petals similar, transversely gibbous and auriculate near the base, conspicuously clawed; stamens usually monadelphous, the anthers versatile; ovary stipitate, oblong, the style cylindrical, the stigma small, capitate. *Fruits* drupaceous, ovoid, the endocarp woody, indehiscent, the seed solitary.

A small genus limited to the tropics of the New World.

The genus *Geoffroea* Jacquin (1763) which predates Aublet's genus (1789) has for its type *G. spinosa* and may include the concept of *Andira,* a *nomen genericum conservandum* over *Vouacapoua.* Jacquin's genus was published a month before Linnaeus' *Geoffraea.* That Linnaeus was influenced by the writings of Jacquin is well-known (cf. A. Robyns' note on *Bombax ceiba* L. in Taxon **10:** 159. 1961). Linnaeus, unfortunately on occasions misspelled Jacquin's names.[5] According to Article 14, note 3 (International Code of Botanical Nomenclature, Regnum Vegetabile **23:** 15. 1961) ". . . When a conserved name competes with one or more other names based on different types and against which it is not explicitly conserved, the earliest of the competing names is adopted in accordance with Art. 57." Thus as *Geoffroea* Jacq. is a non-competing and earlier name, the valid name of the species is: *Geoffroea inermis* W. Wright.

While a substantial argument may be offered for segregating *A. inermis* from *Geoffroea* on the basis of fruit characters I do not regard the evidence as substantial enough. True, the description and the figure of the fruit of Jacquin's *G. spinosa* (loc. cit.) shows that the pericarp has a median longitudinal sulcus which is not found in *A. inermis.* The drupaceous and monospermate fruit of *Geoffroea* has a subovate pericarp which is described as "notata utrinque sulco longitudinali in latere autem compressiusculo. . . ."

1. GEOFFROEA INERMIS W. Wright, Lond. Med. Jour. **8:** 256. 1787.—Fig. 144.

Geoffraea jamaicensis inermis Wright, Phil. Trans. Roy. Soc. London **67:** 512, *t. 10.* 1778.
Andira inermis (W. Wright) H. B. K., Nov. Gen. Sp. Pl. **6:** 385. 1824.
Andira excelsa H. B. K., loc. cit. 385. 1824.
Pterocarpus sapindoides DC., Prodr. **2:** 419. 1825.

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[5] Linnaeus is not to be judged too harshly for his misspelling when one considers that Jacquin altered his name *Goffroea* to *Goeffroea* in a matter of two lines, loc. cit. 207. The majority of taxononists prefer *Geoffroea.*

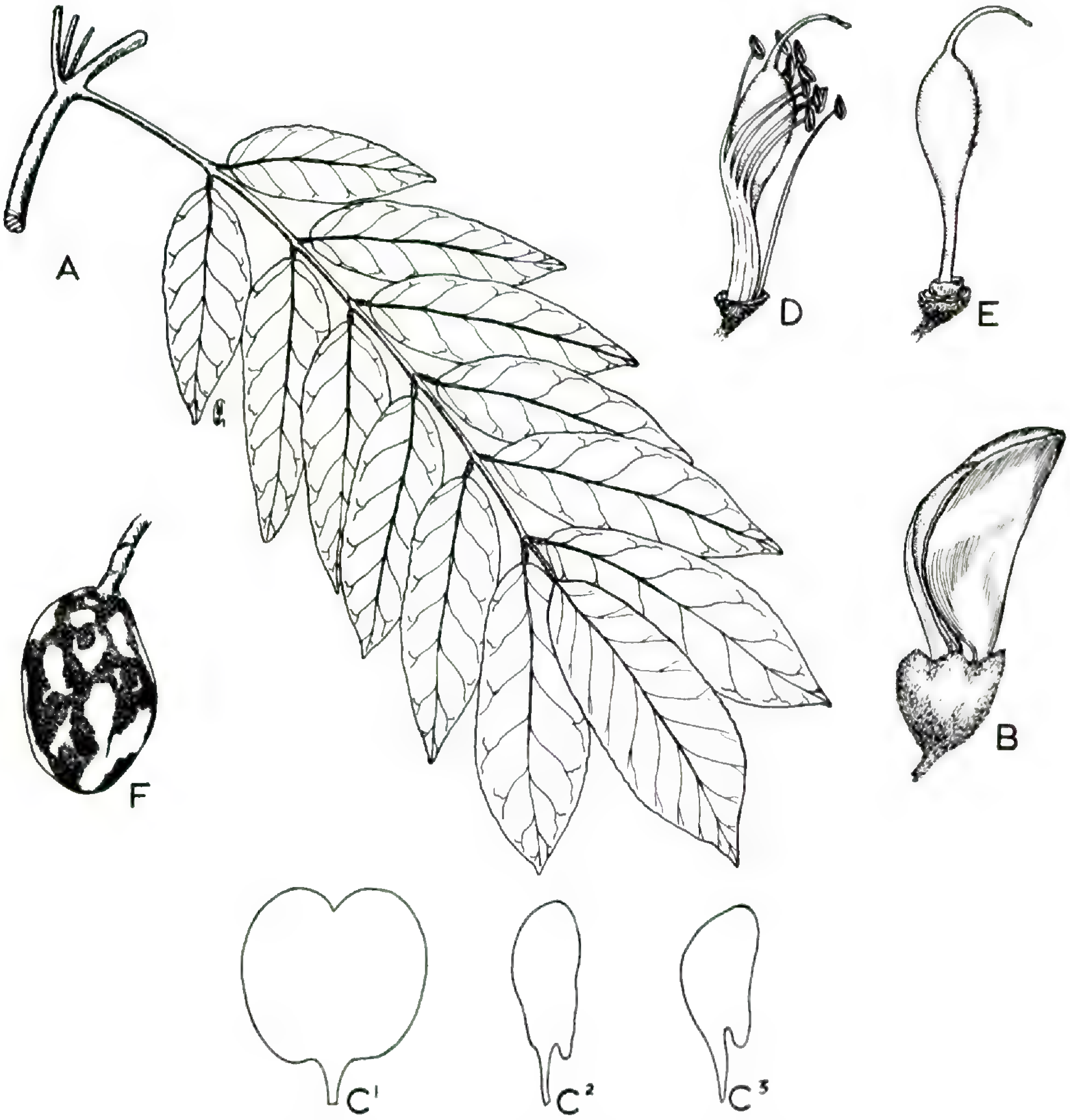

Figure 144. Geoffroea inermis W. Wright: A, leaf (× 5); B, flower (× 5); C, petals (× 4), C[1], vexillum, C[2], wing, C[3], carina; D, androecium (diadelphy) and gynoecium (× 6); E, gynoecium (× 1); F, fruit (× 1). A-E after *Standley 21796* (MO); F after *Broadway s. n.* (MO).

Andira sapindoides (DC.) Benth., Jour. Proc. Linn. Soc., Bot. **4** (Suppl.): 123. 1860.
Andira inermis var. *sapindoides* (DC.) Griseb., Fl. Brit. W. Ind. 202. 1860.
Vouacapoua inermis (W. Wright) Lyons, Plant Names Scientific and Popular 396. 1900.
Andira jamaicensis (W. Wright) Urb., Symb. Ant. **4**: 298. 1905.
Andira chiricana Pittier, Contr. U. S. Nat. Herb. **18**: 235. 1917.

Tree, small. *Leaves* with 7-15 leaflets, these oblong, 2.5-13 cm. long, 1.5-5 cm. wide, variable at the apex, often acuminate for 1.5 cm., chartaceous to subcoriaceous, glabrescent to minutely puberulent along the costa, the latter slender, immersed above, the main veins about 10, the margins subrevolute and usually vaguely crisp; petiolules up to 0.5 cm. long; stipelles subulate, up to 0.6 cm. long; petioles 2-3 cm. long, puberulent; rachises 8-13.5 cm. long; stipules broadly subulate, 0.2-1.0 cm. long, stiff, curled, puberulent. *Panicles* often exceeding the uppermost leaves, the rachises 10-25 cm. long, the basal branches 4-15 cm. long, usually with the secondary branches up to 3 cm. long, twisted, rough with pedicel scars, densely aurous-

puberulent; brachts ovate, about 3 mm. long. *Flowers* subsessile, about 10 mm. long, the hypanthium obliquely campanulate, 3-4 mm. long, thinly carnose, minutely ferruginous-tomentose, glabrous within, the teeth subequal, obscurely or widely triangular, up to 2 mm. long; wing and carinal petals oblong or subreniform, about 6 mm. long, the claw about 3.5 mm. long, thinly carnose, glabrous; staminal sheath about 5 mm. long, gibbous near the tip, glabrous, the filaments up to 3 mm. long, the anthers about 1 mm. long; ovary stipitate for 4-5 mm., elliptic to narrowly obovate, about 3.5 mm. long, sparsely pilose to glabrous, 2- to 3-ovulate, the style subulate, 3.5 mm. long, more attenuate above. *Fruits* obliquely oval, 2.5-5 cm. wide, ligneous.

Common in the tropics of the New World; apparently introduced into parts of East Africa.

BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 147;* Progreso, *Cooper & Slater 265.* CANAL ZONE: Ancón, *Lindsay s.n.;* Barro Colorado Island, *Avilles 920, 981, Bailey & Bailey 52, Bangham 393, 432, Dwyer 1469, Kenoyer 679, Killip 40032, Salvoza 880, 886, Shattuck 375, 393, Starry 205, 227, Wetmore & Abbe 42, 143, 151, Woodworth & Vestal 368, 444;* Ancón, *Mason 13;* France Field, *Mason & Valentine 7044;* Trinidad River, *Pittier 3999;* Navy Pipeline Road, northeast Gamboa Bridge, *Stern 19.* COCLÉ: Río Fató, *Pittier 3870;* El Vallé, *Allen 1770.* DARIEN: El Real, *Duke 4926.*

A. inermis, a common tree in Panama, has conspicuous purple flowers and plump-drupaceous fruits. The fetid bark surrounds a hard wood varying in color from yellow to black; it is used in heavy construction and in ornamental boxes; medicinally the bark is used as a vermifuge and purgative (cf. Standley, Contr. U. S. Nat. Herb. **27:** 218. 1928). In very heavy doses it is a potent poison. Apparently the seeds are poisonous. Johnston (Sargentia **8:** 146. 1949) has interesting notes on flower color: "The standard is usually pink or almost magenta toward the margin, deepening in color and becoming brownish-red about the white center." In addition he appends a lengthy discussion of the nomenclatural history of *A. inermis.* The vernacular name is *cocu.*

I have elected to reduce *A. sapindoides* (DC.) Benth. to synonomy since the only character which may be used to distinguish it is completely glabrous pistil. Numerous dissections of the *A. inermis* complex reveals that there is a great reduction in the indumentum of the ovary, thus suggesting that this is not a strong distinguishing feature.

13. **OLEIOCARPON** Dwyer, gen. nov.

Arbores. Folia imparipinnata jugis foliolorum pluribus oppositis vel approximatis; rhachides saepe alati; stipellae nullae; stipulae minutae caducaeque. *Flores* in crebros terminales racemos conjugati; bracteae parvae deciduaeque; bracteolae 2 calycis maioribus lobis similes et gemmas juveniles valvatim includentes; hypanthium campanulatum, bilabiatum dentibusque (aut lobis) superioribus 2 multo maioribus longioribusque quam dentibus 3 inferioribus, glandulo-punctatum; vexillum subrotundatum, emarginatum; alae carinae petalaque, oblongae, obtusae, alis apice inaequilateraliter bilobatis; stamina 10 monadelpha filamentis alternatim in-

aequilateralibus; ovarium stipitatum, glabrum, stylo breve crasso stigmateque capitato. *Fructus* drupacei, primo pubescentes, indehiscentes, oleaginei monospermatique.

Type species: *Oleiocarpon panamense* (Pittier) Dwyer.

The segregation of this species as a new genus seems justifiable on the grounds that the fruits are obviously structurally different from those of *Coumarouna* Aubl. (Hist. Pl. Gui. Fr. 740. 1775), and the conserved *Dipteryx* Schreb. (in L., Gen. Pl. ed. 8, 485. 1791) (cf. discussion below), although the flowers are strikingly similar. The drupaceous fruits, suggesting the section *Geoffroyeae* of the *Dalbergieae* are pubescent when immature and secrete oil. Ducke, in 4 papers (Arch. Jard. Bot. Río de Janeiro **3:** 142, 162-164. 1922, **4:** 72. 1925; Rev. Bot. Appl. Agric. Trop. **14:** 400-407. 1937; Notiz. Bot. Gart. Berlin **14:** 120-127. 1938) dealing with the genus *Coumarouna* (*Dipteryx*), concludes that *Coumarouna panamensis* was not rightly assigned to the genus, maintaining that the fruits are more like those of *Pterodon*. While they resemble those of *Pterodon* in being oleaginous, they are obviously different in several important respects. The fruit of *Coumarouna* is indehiscent, plump and fleshy, while the fruit of *Pterodon* is thin with the endocarp splitting into valves at maturity. Important too, are differences in foliage, noted a century ago by Bentham (Jour. Proc. Linn. Soc., Bot. **4** (Suppl.): 25-26. 1860): ". . . the leaflets being few, large, and coriaceous in *Dipteryx*, more numerous, smaller, and thinner in *Pterodon*." Pittier, the author of *Coumarouna panamensis*, was skeptical about his choice of genus, remarking in his type description: ". . . it is therefore probable that these species (including *C. panamensis*) ought to represent a new genus, intermediate between *Coumarouna* and *Pterodon*."

The segregation of *C. panamensis* as the type of the new genus serves to by-pass the problem of its original assignment to the genus *Coumarouna* and its subsequent transfer to *Dipteryx* by Record & Mell (Timbers Trop. Am. 303. 1924). *Dipteryx* according to the International Rules, is conserved over *Coumarouna*. This decision, favoring *Dipteryx*, however, apparently assumes that the genus *Taralea* Aubl. (loc. cit. 745. 1775) is included in *Coumarouna*. Ducke in several papers e.g. Trop. Woods **61:** 1-10. 1940) presents convincing evidence that *Taralea* is distinct from *Coumarouna* and maintains that *Coumarouna* deserves to be restored to a state of validity and that *Dipteryx* be invalidated.

1. Oleiocarpus **panamense** (Pittier) Dwyer, comb. nov.—Fig. 145.

Coumarouna panamensis Pittier, Contr. U. S. Nat. Herb. **18:** 236. 1917.
Dipteryx panamensis (Pittier) Record & Mell, Timbers Trop. Am. 303. 1924.

Tree, tall. *Leaves* with 24-28 leaflets, the uppermost pair usually located 1-3 cm. below the tip of the rachis, the lowermost pair apparently opposite, with the bases contiguous on the upper side of the rachis, oblong, up to 21 cm. long, up to 8 cm. wide; petiolules up to 0.9 cm. long; petioles about 8 cm. long, up to 0.8 wide, swollen at the base, involute; rachises up to 37 cm. long, alate, papillate, glabrous; stipules caducous. *Panicles* terminal, up to 40 cm. long, the branches patulous,

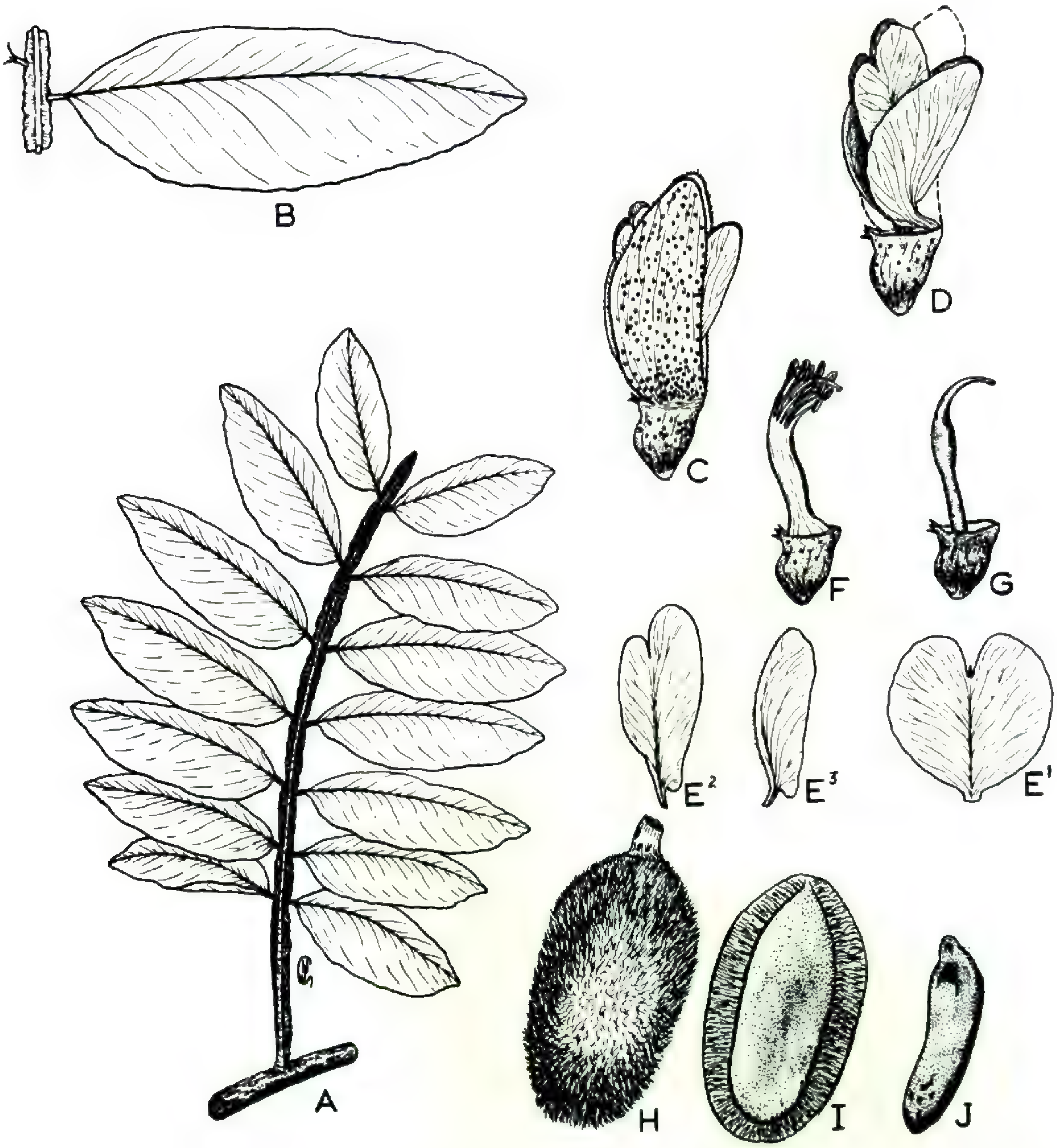

Figure 145. OLEIOCARPON PANAMENSE (Pittier) Dwyer: A, leaf (× ½); B, leaflet (× 1); C, flower (× 3); D, flower with a calyx lobe removed (× 3); E, petals (× 3), E¹, vexillum, E², wing, E³, carina; F, androecium (monadelphy) and receptacle cup (× 3); G, pistil (× 3); H, fruit, surface view (× 1); I, fruit in hemisection, internal view, without seed (× 1); J, seed (× 1). A-G after *Stern, Chambers, Dwyer & Ebinger* 973 (MO); H-J after *s. coll. s. n.* (US 866002).

arcuate, pubescent; pedicels 4-5 mm. long, expanded at the apex. *Flowers* with the hypanthium about 10 mm. long, with 2 very conspicuous oblong lobes, 8-20 mm. long, up to 4 mm. wide, obtuse, puberulent within, glandular-punctate, the remaining 3 lobes (teeth) minute, falcately uncinate, up to 1 mm. long, the margins irregular at the apex lanulose within; vexillum subsessile, rotund, 6-10 mm. long, emarginate, often with a conspicuous tooth in the sinus, subobtuse and carnose at the base; carinal petals inequilaterally oblong, up to 6.5 mm. long, 3-6 mm. wide, puberulent along the lower margin, a conspicuous vein paralleling the lower margin; stamens with the sheath 8-14 mm. long, glabrous, the filaments subequal, up to 3.5 mm. long, the shorter anthers about 0.5 mm. long, the longer anthers about 0.7 mm. long; pistil flat, about 4 mm. long, the style about 2 mm. long, glabrous, the stigma truncate. *Fruits* pedicellate for about 1.5 cm.; plump, drupaceous, oleaginous, elliptic, about 6 cm. long, about 3 cm. thick and wide, obtuse, at first with a gray-green pubescence, the hairs soon deciduous; seed somewhat flat, almond-shaped, about 5 cm. long, about 1.5 cm. wide, light brown.

Known only from Costa Rica, Panama, and Colombia.

BOCAS DEL TORO: Chiriquí Land Co., 11 m. west of Almirante, *Stern 108;* Water Valley, Chiriquí Lagoon, *von Wedel 757.* CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 71, Fairchild s. n., Standley 31439, 41074;* Trinidad River, *Pittier 4033.* DARIEN: headwaters of Río Chico, *Allen 4608;* Boca de Pauarando on Sambu River, *Pittier 5257;* El Real, *Stern, Chambers, Dwyer & Ebinger 973.* PANAMA: La Chorrera, *Allen 3612;* Arraijan, *Cook & Martin 45;* Arenoso, lower Río Trinidad, *Seibert 619.*

When in flower the tree is one of the most attractive in the forest, its crown of terminal panicles dense with pink-purple blossoms readily visible at considerable distances from the rivers. The flowers persist for weeks; on falling to the forest floor they attract leaf-cutting ants. The wood is extremely hard and is avoided by axe-men. According to Standley (under the name of *Coumarouna panamensis,* Contr. U. S. Nat. Herb. **27:** 219. 1928), as the fruits dry their oily liquid crystallizes. Apparently the kernals of the seeds may be eaten before roasting. The vernacular name is *almendro.* The fragrant seeds are known as *tonka beans.*

Marsh, in his "White Indians of Darien" (96-97. 1934), observed that the Indians used the fruits to make torches: "they consist of about 20 nuts of the *almendra* tree, rather like nutmegs in shape and size. They are strung tight against each other on a long sliver of black palm and give a light about as bright as a common kerosene lantern. As one nut is consumed, it lights up the next one. . . . Each nut burned for about 5 minutes."

(to be continued)

FLORA OF PANAMA[1]

Part VI

Family 92. MELIACEAE[2]

By C. Earle Smith, Jr.

Trees or shrubs. *Leaves* alternate, rarely otherwise, usually pinnately or palmately compound, occasionally simple, estipulate; leaflets generally entire, at times with pellucid lines or dots. *Inflorescence* axillary or terminal, usually paniculate. *Flowers* regular, perfect, rarely polygamodioecious, 4- to 6-merous, but basically 5-merous; calyx and corolla either imbricate or valvate; petals free or rarely barely connate or adnate to the lower part of the staminal tube or gynophore; stamens usually twice as many as the petals, sometimes only as many as the petals, rarely more than twice as numerous, usually united partly or wholly into a tube; anthers 2-celled, longitudinally dehiscent; disk sometimes wanting, usually annular or cupular, free or adnate to the androecium or gynoecium; ovary of 2-6 united carpels, 2- to 12-celled; stigma discoid or capitate, simple or sulcate; ovules 2 or more in each cell, collateral or superposed, rarely solitary. *Fruit* capsular, septicidally or loculicidally dehiscent, sometimes drupaceous or baccate; seeds solitary to numerous in each cell, sometimes winged; endosperm carnose or none; embryo straight or transverse, the cotyledons fleshy or foliaceous; radicle superior or lateral.

A family of about 45 genera in the tropics and subtropics of both hemispheres. Among the trees are a number of species widely cut for lumber. In the American tropics the preferred sources of lumber are mahogany or *caoba* (*Swietenia* spp.) and Spanish cedar or *cedro* (*Cedrela* spp.) in that order followed by the many other trees cut for lumber. Mahogany, *cedro* and the Asiatic china-berry (*Melia Azederach L.*) are widely planted as ornamentals while *cedro* has also been used as a coffee shade tree and has been widely planted for reforestation.

The taxonomy of several of the American genera is in chaotic condition with many more species names in the literature than exist among the herbarium specimens. In order to arrive at the probably correct names for Panamanian species of *Guarea* and *Trichilia,* all of the Panamanian material of these and other Meliaceous genera from the Harvard University Herbaria, the U. S. National Herbarium, and the herbarium of the Missouri Botanical Garden were compared with the large collection of American *Meliaceae* at the Chicago Natural History Museum. Where types were available and the interpretation of the species was secure, reductions

[1] The Flora of Panama by Robert E. Woodson, Jr. and Robert W. Schery and Collaborators should be cited as: Ann. Missouri Bot. Gard., with volume number, pagination and date of the Annals.

[2] Assisted by National Science Foundation Grants No. G-7144 (Principal Investigator, R. E. Woodson, Jr.) & GB-170 (Principal Investigator, H. C. Cutler).

Ann. Missouri Bot. Gard. **52**: 55-79. No. 1. 1965.

were made as indicated in the synonymic lists in this paper. In all cases, the oldest name to which the taxon could be confidently assigned was used, but later study may find these judgments in error. Loans of authentic specimens of *Guarea glabra* Vahl from the Botanical Museum of Copenhagen and of *Trichilia tomentosa* H. B. K. and *T. montana* H. B. K. from the *Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle* of Paris are particularly appreciated.

a. Leaves 2- to 3-pinnate; fruit drupaceous, flowers purple. .... 1. MELIA
aa. Leaves once pinnate or, rarely, 1- to 3-pinnate 3-foliate; fruit capsular or subbaccate; petals not purple.
 b. Filaments not connate; seeds winged. .... 2. CEDRELA
 bb. Filaments united for all or part of their length; seeds winged only in *Swietenia*.
  c. Seeds bearing a large wing; disk cupular, thin. .... 3. SWIETENIA
  cc. Seeds not winged, arillate except in *Carapa;* disk annular or columnar.
   d. Capsule dehiscent from the base upward; seeds not arillate; disk annular, carnose. .... 4. CARAPA
   dd. Capsule dehiscent from the apex downward; seeds arillate; disk thin-annular, columnar or obsolete.
    e. Disk annular; anthers borne at the apex of the staminal tube. .... 5. TRICHILIA
    ee. Disk columnar or obsolete; anthers included in the staminal tube. .... 6. GUAREA

1. MELIA L.

MELIA L., Sp. Pl. 384. 1753.

Azederach Mill., Gard. Dict. Abridg. ed. 4. 1754.
Azedara Raf., Fl. Ludov. 135. 1817.

Trees. Leaves alternate, pinnate or bipinnate, leaflets entire or, usually, dentate. *Inflorescence* an axillary panicle. *Flowers* purple, showy, 5- to 6-merous; petals contorted, spreading; staminal tube cylindric, dilated above, 10- to 12-dentate, each tooth cleft; anthers 10-12, included; disk annular; ovary 3- to 6-celled; stigma 5- to 6-lobate; ovules 2 in each cell, superposed. *Fruit* a drupe enclosing a 1- to 6-celled stone; seeds usually solitary in each cavity; endosperm carnose; cotyledons foliaceous, radicle terete, superior.

Old World trees largely restricted to the tropics and subtropics.

1. MELIA AZEDERACH L., Sp. Pl. 384. 1753.—Fig. 1.

Tree to 10 m. *Leaves* usually bipinnate, leaflets numerous, lanceolate to oval, 3-8 cm. long, the base acute to subcordate, the apex acute to acuminate, incised-serrate or lobate. *Inflorescences* 10-25 cm. long. *Flowers* slender-pedicellate; sepals 2-3 mm. long, lanceolate to ovate; petals purple or whitish, 8-12 mm. long; staminal tube deep purple; ovary glabrous. *Drupes* globose, 1.5-2 cm. in diam., translucent-yellow; pit bony, sulcate.

A tree long in cultivation throughout the warm areas of the world; it occasionally escapes into hedgerows and along roadsides.

BOCAS DEL TORO: Almirante, *Cooper 43.* CHIRIQUÍ: Progreso, *Cooper & Slater 290.* CANAL ZONE: Cocoli, *Riley 131.*

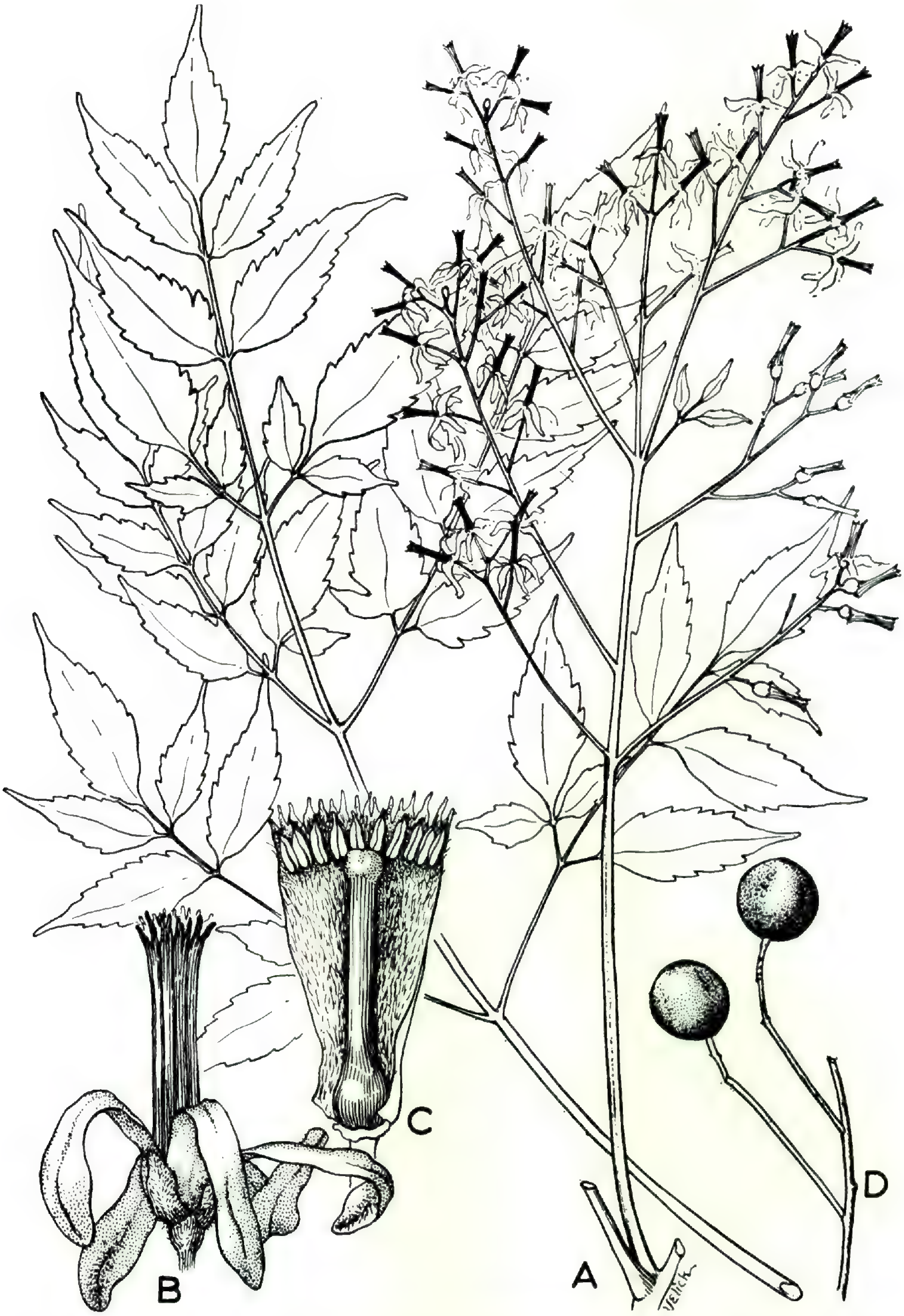

Figure. 1. MELIA AZEDERACH L.: A, leaf and inflorescence (ca. × ⅔); B, flower (× 3⅓); C, id., calyx and petals removed, the androecium opened (ca. × 3⅓); D, fruits (ca. ×⅔).

2. CEDRELA P. Br.

Cedrela P. Br., Civ. Nat. Hist. Jamaica 158. 1756.

Cedrus Mill., Gard. Dict. ed. 7. 1759.
Johnsonia Adans., Fam. Pl. **2:** 343. 1763.
Pterosiphon Turcz., Bull. Soc. Imp. Nat. Mosc. **36**(1-2):589. 1863.
Surenus O. Ktze., Rev. Gen. Pl. **1:** 110. 1891.

Trees to 60 m. tall; trunk buttressed on old and large trees; branchlets sometimes conspicuously lenticellate. *Leaves* alternate, paripinnately compound, very variable in length, the leaflet pairs variable in number, 8-20 pairs, opposite or subopposite; leaflets ovate to lanceolate, generally acuminate, glabrous to densely pubescent, the margin entire, very variable in size and shape. *Inflorescence* terminal, pyramidal, paniculate, the branches generally at right angles to the axis. *Flowers* perfect, (4-) 5 (-6)-merous; calyx cupulate or lobed; petals spatulate to lanceolate and adnate to the gynophore along their lower $\frac{1}{3}$, entire, frequently fleshy; stamens with fleshy filaments adnate to the gynophore below, free above, as long as or shorter than the corolla; anthers introrsely dehiscent through a slit, the connective frequently prolonged into an apiculum; pistil borne at the apex of a gynophore, the ovary 5-celled with ovules hanging in 2 rows per cell on the central column; stigma capitate. *Fruit* a septicidally dehiscent capsule opening cleanly from the apex; seeds hanging from the thick central column, numerous, the seed coat continued as a membranous wing from the apex of the seed.

Cedrela is restricted to the American tropics from Mexico to Argentina where six species and possibly a seventh species are recognized.

a. Calyx cupulate, split on one side, variously, but not deeply, dentate; capsule less than 5 cm. long, the valves 1-2 mm. thick.
  b. Leaflets strongly oblique at the base, often glabrous; calyx usually glabrous, irregularly dentate; petals thin, evenly light in color; column in the capsule with wings extending to the base of the broad apex. .... 1. C. odorata
  bb. Leaflets slightly oblique at the base, puberulent to pubescent, particularly along the veins beneath; calyx puberulent, generally regularly 5-dentate; petals moderately thick, often darker in color at the apical margin; column in the capsule with wings extending to the base of the narrow apex. .... 2. C. angustifolia
aa. Calyx regularly and deeply 5-lobate; capsule usually exceeding 6 cm. in length, the valves 2-3 mm. thick. .... 3. C. tonduzii

1. Cedrela odorata L., Syst. Nat. ed. 10, 940. 1759.

Cedrela guianensis A. Juss., Mém. Mus. Hist. Nat. Paris **19:** 295. 1830.
Cedrela mexicana M. J. Roem., Fam. Nat. Regni Veg. Syn. Monogr. **1:** 137. 1846.

Tree to 40 m.; branchlets generally glabrous, occasionally conspicuously lenticellate, more often with small lenticels. *Leaves* with 5-11 pairs of leaflets 8-17 cm. long by 2.5-5.5 cm. wide, broadly lanceolate to ovate, the base acute to rounded, often markedly oblique, the apex acuminate obtuse, rarely acute, sometimes mucronulate, generally glabrous, occasionally puberulent or short pubescent along the veins beneath. *Inflorescences* open, variable in size, often shorter than the leaves, usually glabrous, rarely puberulent, the bracts caducous. *Flowers* 6-9 mm. long;

calyx cupulate and split on one side, 1.5-3 mm. deep, the margin generally shallowly and irregularly toothed, glabrous, rarely puberulent, light to dark in color; petals elliptical to subspatulate, puberulent without, uniformly light in color; filaments of the stamens thick but usually of uniform diam., the anthers short apiculate, 0.75-1.5 mm. long; ovary hemispherical to ovoid, usually glabrous, 1-2 mm. long, style 1.5-2 mm. long, the capitate stigma about 0.5 mm. thick. *Fruit* 2.5-4.5 cm. long, the valves thin, the central column with wings extending to the base of the broadened apex.

Trees of dry to moist soils at lower elevations, frequent in second-growth forest but largely cut before attaining a very large trunk diameter. The species ranges from the West Indies and northern Mexico to the Amazon drainage of Brazil but it is largely restricted to the area of Caribbean drainage in Panama. It is frequently planted as a street tree.

CHIRIQUÍ: Progreso, *Cooper & Slater 306.*

Wherever *C. odorata* is growing in close proximity to *C. angustifolia*, hybridization can be expected between the two species. The progeny will not separate clearly into either species on any character currently known to me. To date the *cedros* collected in Panama have not shown this intermixing, but it is certainly to be anticipated as more specimens become available.

2. CEDRELA ANGUSTIFOLIA Sessé & Moç. ex DC., Prodr. **1:** 624. 1824.

Cedrela brasiliensis A. Juss. in St.-Hil., Fl. Bras. Merid. **2:** 86, *t. 101.* 1829.
Cedrela fissilis Auct. non Vell.

Tree to 60 m., usually 30 m. or less, with upright branches and an open crown; branchlets with small lenticels, glabrous or glabrate. *Leaves* with 5-10 pairs of leaflets 9-25 cm. long by 3-8.5 cm. wide, elliptical to ovate to ovate-lanceolate, seldom lanceolate, the base subacute to rounded, slightly oblique, the apex obtuse to long-acuminate, pubescent along the midrib above, scantily puberulent to thickly pubescent and scattered hirsute, primarily on the veins and venules below, sometimes glabrous or with the axils of the secondary veins barbate. *Inflorescences* variable in size, often about equalling the length of the leaves, usually puberulent; bracts caducous. *Flowers* 6-9 mm. long; calyx shallowly cupulate and usually split at one side, 2-3 mm. deep, the margin irregularly shallowly lobed to definitely 5-lobed, often scattered puberulent, dark in color; petals elliptical, densely pubescent, reddish near the apex; filaments of the stamens fleshy, the anthers apiculate, 0.8-1.9 mm. long; ovary 1-1.5 mm. long, hemispherical, puberulent; style 1.5-3 mm. long, thick, puberulent; capitate stigma about 0.5 mm. thick, glabrous. *Fruit* 2.5-5 cm. long, the valves thin (to 1.5 mm. thick), the central column with 5 conspicuous wings extending nearly to the narrow apex.

Trees of dry to moist sites at less than 2,000 m. elevation, conspicuous in second-growth before they are cut, ranging from northern Mexico to northern Argentina. Frequently planted as ornamental trees.

CHIRIQUÍ: Progreso, *Cooper & Slater 252, 305.* DARIEN: vicinity of El Real, Río Tuira, *Stern, Chambers, Dwyer & Ebinger 745.* HERRERA: Ocú, *Allen 4082.* COCLÉ: Aguadulce, *Pittier 4985.* CANAL ZONE: Curundú, *Harvey 5256, Smith & Smith 3254.* PANAMA: Alhaguela, *Pittier 3729;* Cerro Campana, *Allen 2081;* Punta Paitilla, *Standley 30793;* San José Island, *Erlanson 303, Johnston 323;* Soto Caballo, *Smith, Smith & Arauz 3322;* Guayabito, *Smith & Smith 3448.*

3. Cedrela tonduzii C. DC., Bull. Herb. Boiss., ser. 2, **5:** 427. 1905.

Cedrela salvadorensis Standley, Field Mus. Nat. Hist., Bot. Ser. **4:** 215. 1929.

Tree to 40 m. (fide *Little* 6077); branchlets often thick, sometimes conspicuously lenticellate. *Leaves* with 5-7 pairs of leaflets 7.5-14 cm. long by 2.5-6.0 cm. wide, lanceolate to elliptical, the base acute to rounded, subequilateral, the apex acuminate obtuse to acute, rarely glabrate, the veins usually pubescent above, the lower surface densely puberulent to pilose. *Inflorescences* sometimes dense, usually shorter than the leaves, puberulent; bracts subpersistent, to 1.5 mm. long, puberulent. *Flowers* 5-7 mm. long; calyx shallowly to deeply 5-lobed, occasionally split to the base on one side, 1-1.5 mm. deep, generally puberulent; petals elliptical, thickened at the center, puberulent to short pilose without, light at the base shading to rose at the apex along the margins; stamens with the filaments thick-fleshy where they are adnate to the gynophore, narrowing abruptly above, the connective wide, ending in a marked apiculum, the anthers 1-1.9 mm. long; ovary ovoid, glabrous; style usually 2-3 mm. long, glabrous; capitate stigma usually about 0.75 mm. thick. *Fruit* 6-10 cm. long, the valves heavy, usually at least 2 mm. thick, the outer surface lenticellate, smooth; central column with 5 wings extending to the apex over the broad end, the scars from seed attachment extending basally about $\frac{1}{3}$ the length of the column.

Trees of moist areas at elevations up to 2,000 m., ranging from Chiapas, Mexico to Chiriquí Province in Panama.

CHIRIQUÍ: Río Chiriquí Viejo, *Little 6077;* near Finca Lerida, *Allen 4751.*

In my monograph on *Cedrela* (Fieldiana: Bot. **29:** 295-341. 1960) this species is confused with *C. oaxacensis* C. DC. & Rose. Since that time, Dr. Faustino Miranda has kindly brought to my attention specimens showing that the large capsules of *C. tonduzii* are produced several together on a hanging inflorescence. Previous collections have only single detached capsules with no indication of the shape of the fruiting inflorescence. *C. tonduzii* is generally restricted to moist, evergreen forests, whereas *C. oaxacensis* is a tree of deciduous forests in southern Mexico.

3. SWIETENIA Jacq.

Swietenia Jacq., Enum. Syst. Pl. 4, 20. 1760.

Mahogani Adans., Fam. Pl. **2:** 343. 1763, pro parte.
Roia Scop., Intr. Hist. Nat. 226. 1777.

Trees. Leaves alternate, pari- (rarely impari-) pinnate; leaflets 2-6 pairs, opposite, inequilateral, entire. *Inflorescences* axillary, paniculate. *Flowers* whitish,

(4-) 5-merous; calyx lobed, imbricate; corolla imbricate; staminal tube urceolate, 10-dentate, the anthers 10, included; disk cupulate, the margin crenulate; ovary sessile in disk, glabrous; stigma discoid; ovules numerous in each cell, pendulous. *Fruit* large, capsular, septicidally dehiscent from the base, the valves separating into 2 layers, adnate to the central column at the apex; seeds numerous in each locule, the seed-coat developed into a large wing between the placenta and the seed; endosperm thin, carnose; embryo transverse, the cotyledons large, the radicle short.

A genus of three closely related species of which only one is represented by herbarium specimens from Panama.

1. SWIETENIA MACROPHYLLA G. King in Hook., Icon. Pl. **16:** *t. 1550.* 1886.—Fig. 2.

Tree to 30 m. *Leaves* to 30 cm. long, largely paripinnate; leaflets 3-5 pairs, opposite, 6-14 cm. long, 3-6 cm. wide, inequilateral, ovate to elliptical, the base obtuse to acute, the apex acuminate, acute. *Inflorescences* axillary, 10-20 cm. long or longer, glabrous. *Flowers* usually 5-merous; calyx 2-2.5 mm. in diam., the lobes rounded; petals obovate, white; staminal tube cylindric-urceolate, the teeth acute or acuminate. *Capsule* ovoid, 12-15 cm. long, to 7 cm. in diam.

Moist forests of the Caribbean watershed of Mexico and Central America, southward into Brazil and Peru. The mahogany trees or *caobas* have been very thoroughly harvested in all accessible localities in Panama and it is now impossible to ascertain its former distribution. Probably the smaller *caoba* of the Pacific side of Mexico and Central America formerly came into Panama, but it grew in the more open forests of better-drained areas which would have been easily logged.

PANAMA: Juan Díaz, *Fisher 3, 4, 11.*

4. CARAPA Aubl.

CARAPA Aubl., Hist. Pl. Gui. Fr. Suppl. 32. 1775.

Persoonia Willd. in L., Sp. Pl. ed. 4 [i.e. 5], **2:** 331. 1799.
Amapa Steud., Nom. Bot. ed. 1, 69. 1821.
Granatum O. Ktze., Rev. Gen. Pl. **1:** 110. 1891.

Trees. Leaves alternate, pari- or impari-pinnate; leaflets entire, usually coriaceous. *Inflorescences* terminal or axillary. *Flowers* perfect, 4- to 5-merous; sepals imbricate; petals free, alternate with the sepals; staminal tube cupular or ovoid, 8- to 10-lobate, the lobes cleft or entire; anthers 8-10, sessile within the tube at the base of the sinuses; disk annular, carnose; ovary sessile, 4- to 5-sulcate, 4- to 5-celled; style short; stigma discoid; ovules 2-8 in each cell, biseriate or superposed. *Fruit* a large capsule, 1- to 5-celled, subglobose or ovoid, ligneous or carnose, the cells 2- to 5-seeded; seeds large, angulate, without endosperm, the testa corky; radicle lateral.

Several species are known from tropical America and Africa. The following descriptions and citations have been modified from a manuscript sent to the author

Figure 2. Swietenia macrophylla G. King: A, leaves (ca. × 2/3); B, inflorescence (ca. × 2/3); C, flower bud (ca. × 6 2/3); D, flower (× ca. 3 1/2); E, seed (ca. × 1/2).

by Dr. Hugh Iltis, University of Wisconsin, Madison, who has been interested in this genus for some years. The use of this material is very much appreciated.

a. Flowers sessile; sepals and petals glabrous; developing structures at branch tip glabrous to scurfy. ....1. C. GUIANENSIS
aa. Flowers pedicellate; sepals and petals usually puberulent or tomentose; developing structures at branch tip brown-tomentose. ....2. C. NICARAGUENSIS

1. CARAPA GUIANENSIS Aubl., Hist. Pl. Gui. Fr. Suppl. 32, *tab.* 387. 1775.

Persoonia guareoides Willd. in L., Sp. Pl. ed. 4 [i.e. 5], **2:** 331. 1799.
Amapa guinaensis (Aubl.) Steud., Nom. Bot. ed. 1, 69. 1821.
Granatum guianense (Aubl.) O. Ktze., Rev. Gen. Pl. **1:**110. 1891.
Guarea mucronulata C. DC., Notizbl. K. Bot. Gart. Mus. Berlin **7:** 499. 1917.

Tree, medium to large, up to 50 m. tall. *Leaves* crowded at the ends of the branches, paripinnate, 24-60 cm. long; leaflets 3-7 (-9) pairs, elliptic-oblong or ovate-oblong to narrowly lanceolate or oblanceolate, the base cuneate to rounded, the apex rounded, apiculate or cuspidate, sometimes rounded to acute or acuminate, 11-48 cm. long, 3.5-15.5 cm. wide, glabrous on both surfaces. *Inflorescences* axillary, paniculate; bracts and bracteoles persistent, glabrous. *Flowers* white to yellowish or greenish, also dull red or purple, sessile to subsessile, 4-5 mm. long, 4-merous; sepals rounded or broadly ovate; petals imbricate in bud; staminal tube cupulate to urceolate, 8-toothed, the teeth truncate, emarginate or irregularly toothed; anthers 8; disk shallow or concave and ridged; ovary 4-angulate, 4-celled; ovules 2 per cell. *Fruit* globose, 4-ridged, sometimes warty on the ridges; seeds 7-8, dark brown.

Moist forests particularly along rivers from the West Indies and British Honduras to Brasil. While no specimens have been collected from Panama, its presence in Costa Rica and Colombia indicates that this species is to be found in the forests of the Caribbean watershed of Panama.

2. CARAPA NICARAGUENSIS C. DC., Monogr. Phaner. **1:** 717. 1878.—Fig. 3.

Granatum nicaraguense (C. DC.) O. Ktze., Rev. Gen. Pl. **1:** 110. 1891.
Carapa Slateri Standley, Trop. Woods **10:** 48. 1927.

Tree, medium to large, up to 30 m. tall. Leaves pari- or impari-pinnate, 32-66 cm. long, the rachis lenticellate and terminated by a glandular, tomentose projection in the absence of a terminal leaflet; leaflets 4-6 (-7) pairs, oblanceolate, the base cuneate to rounded, the apex broadly acute to rounded or retuse with a small, tomentose mucro, 8.5-48 cm. long, 4.5-15 cm. wide, the veins brown-tomentose, the blades scattered tomentose above and below. *Inflorescences* axillary, paniculate, tomentose; bracts and bracteoles persistent, tomentose. *Flowers* subsessile or pedicellate, white, aromatic, 0.7-4 mm. long, 4-merous; sepals suborbicular to ovate, tomentose or glabrate; petals dotted with 1-2 glands on the outside; staminal tube urceolate, 8-toothed, the teeth truncate-emarginate, or broadly bifid; anthers 8; disk fleshy; ovary 4-angulate, 4-celled; ovules 2 per cell. *Fruit* cylindrical, to 16 cm. long, 4-valved; seeds yellow-ochre, rarely brown with whitish specks.

Lowland forest from Nicaragua to Ecuador.

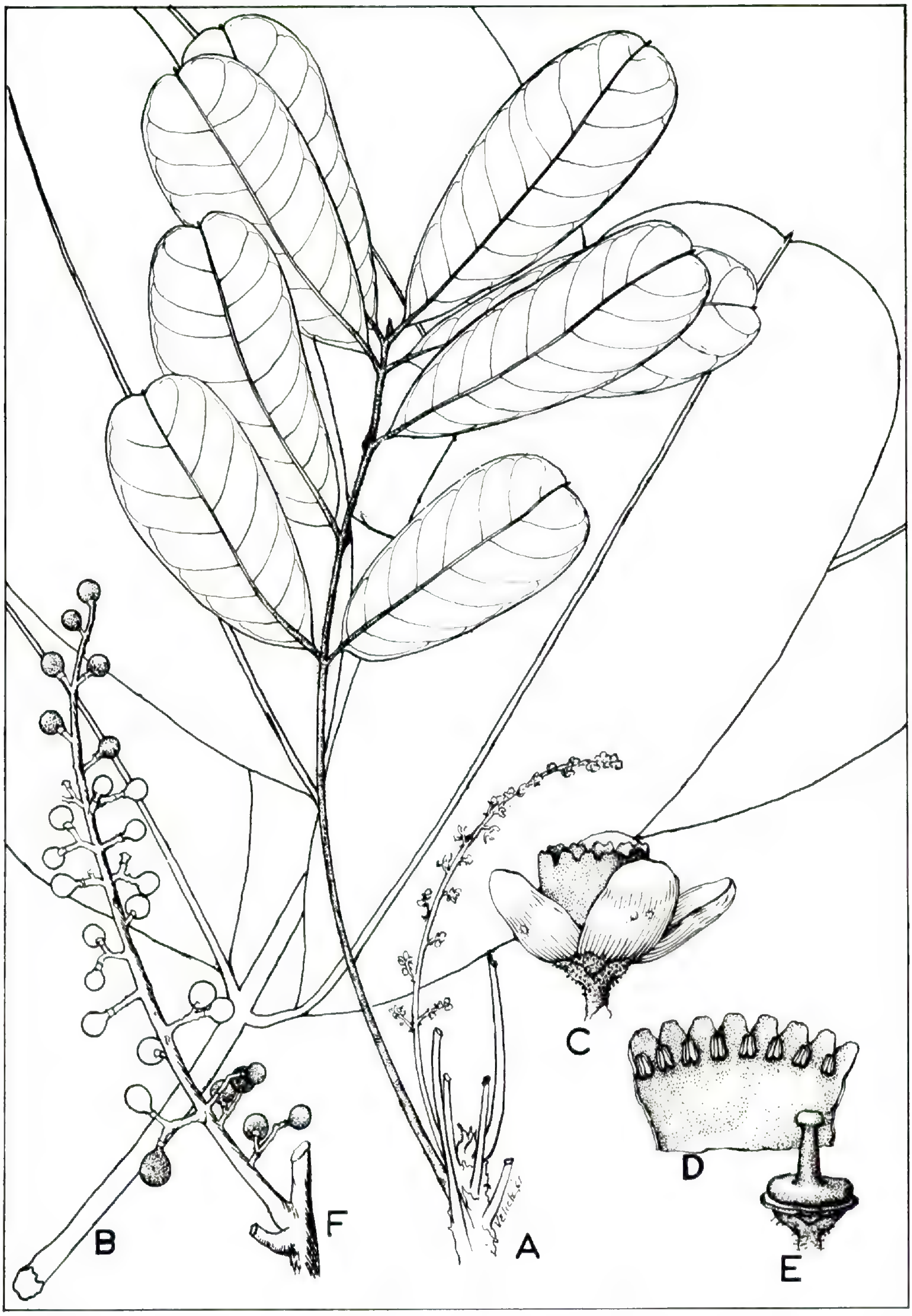

Figure 3. Carapa nicaraguensis C. DC.: A, habit (ca. × ½); B, mature leaf (ca. × ⅓); C, flower (ca. × 6); D, staminal tube opened (ca. × 6); E, gynoecium (ca. × 6); F, very young fruits (ca. ⅓).

BOCAS DEL TORO: Changuinola Valley, Almirante region, *Cooper & Slater 59, 59a;* vicinity of Guabito between Changuinola River and Simaola River, *Stern & Chambers 116;* Comarca del Barú, Puerto Armuelles between Canazo and Cocos, *Cooper & Slater 282.* CANAL ZONE: 2 miles south of Fort Sherman, *Johnston 1824.* DARIEN: Punta Guayabo Chiquita, *Stern & Chambers 166;* along Río Tuira below El Real and Piriaque Island, *Stern, Chambers, Dwyer & Ebinger 969.*

5. TRICHILIA L.

TRICHILIA L., Syst. Nat. ed. 10, 1020. 1759.

Portesia Cav., Mon. Cl. Diss. Dec. **7**: 369. 1789.
Odontandra Roem. & Schult. in L., Syst. Veg. ed. 16, **5**: 511. 1819.
Moschoxylum A. Juss., Mém. Mus. Hist. Nat. Paris **19**: 238. 1830.
Acrilia Griseb., Fl. Brit. W. Ind. Isl. 129. 1859.
Pholacilia Griseb., loc. cit. 129. 1859.
Acanthotrichilia (Urban) Cook & Collins, Contr. U. S. Nat. Herb. **8**: 65, 238. 1903.

Trees or shrubs. *Leaves* alternate, odd- or even-pinnate, trifoliolate or, rarely unifoliolate; leaflets opposite or alternate, usually entire (but spiny-margined in a few species of the West Indies). *Flowers* hermaphroditic in axillary (terminal?) panicles; calyx flat or cupulate, 4- to 5-lobed or the sepals nearly distinct; petals (3-) 4-5, free or connate at the base, imbricate or valvate; stamens 4 to usually 8 or 10, the filaments generally broad and united at or above the base, sometimes with a pair of processes at either side of the anther; anthers always terminal and erect; ovary 2- or 3-celled, sometimes short-stipitate; stigma capitate or disk-like, 2- to 3-lobed; ovules 1 or 2 per cell, laterally paired or superposed. *Fruit* 2- or 3-loculed, loculicidally dehiscing from the apex, the locules 1- or 2-seeded; seeds inverted; testa thin, coriaceous; cotyledons fleshy; radicle superior.

The distinctions between species of *Trichilia* are frequently very tenuous. Some 200 species of tropical America and Africa have been proposed, but the American species probably number less than 50.

Occasionally there is a conspicuous annular disk within the flower which may be adnate to the staminal ring or the ovary.

a. Staminal tube entire, the anthers may alternate with apicula.
  b. Leaf-rachis to 15 cm. long; leaflet-apex rounded or obtuse, rarely acuminate. .... 1. T. GLABRA
  bb. Leaf-rachis 20-40 cm. long; leaflet-apex acuminate to acuminate-obtuse in *T. Cibo* and/or the midrib markedly raised on the upper leaf-surface.
    c. Calyx of nearly free, imbricate sepals. .... 2. T. MORITZII
    cc. Calyx lobed, the lobes never imbricate.
      d. Staminal tube about $\frac{1}{2}$ the height of the petals; stigma thick-capitate; capsule smoothly velutinous. .... 3. T. JAPURENSIS
      dd. Staminal tube $\frac{2}{3}$-$\frac{3}{4}$ the height of the petals; stigma disk-like; capsule glabrous, muricate. .... 4. T. CIPO
aa. Staminal tube lobed for $\frac{1}{3}$ or more of its height.
  e. Leaf-rachis 1-1.5 cm. long; leaves 1- to 3-foliate. .... 5. T. TRIFOLIA
  ee. Leaf-rachis much longer; leaflets 2 or more pairs.
    f. Inflorescences less than 4 cm. long, sometimes appearing to be fascicled; capsule ellipsoidal, usually golden-velutinous. .... 6. T. MONTANA
    ff. Inflorescences 5 cm. long or longer; capsule sphaeroidal or obpyramidal, reddish-velutinous.
      g. Inflorescences racemose; capsule usually 2- to 4-seeded. .... 7. T. HIRTA
      gg. Inflorescences paniculate, sometimes crowded; capsule usually 1-seeded. .... 8. T. TOMENTOSA

Figure 4. TRICHILIA GLABRA L.: A, habit (× 1); B, flower (× 8); C, staminal tube opened and gynoecium (× 8); D, gynoecium (× 16).

1. TRICHILIA GLABRA L., Syst. Nat. ed. 10, 1020. 1759.—Fig. 4.

Trichilia havanensis Jacq., Enum. Syst. Pl. 20. 1760.
Trichilia emarginata C. DC., Monogr. Phaner. **1**: 701. 1878.
Trichilia Oerstediana C. D.C., loc. cit. 677. 1878.
Trichilia Donnell-Smithii C. DC., Bot. Gaz. **19**: 2. 1894.
Trichilia alajuelana C. DC. in J. D. Sm., Enum. Pl. Guatemal. **5**: 13. 1899, *nom. nud.*
Trichilia Davidsoniae Standley, Field Mus. Nat. Hist., Bot. Ser. **22**: 85. 1940.

Shrub or small tree to 8 m. tall, rarely a larger tree. *Leaves* to 15 cm. long; leaflets 2-5 pairs borne oppositely on the rachis, occasionally imparipinnate; blades 2.5-14 cm. long, 1.5-7 cm. wide, obovate, sometimes nearly cuneate, elliptical or nearly lanceolate, the base acute, the apex rounded to obtuse, rarely acuminate, glabrous to pubescent along the midrib above and along the veins beneath. *Inflorescences* axillary, short-racemose, usually less than 3 cm. long. *Flowers* white or greenish, 2-3 mm. long, 4- to 6-merous; calyx nearly flat, the lobes deltoid, glabrous to pubescent without, glabrous within; petals ovate to lanceolate, thin, glabrous to to short-scattered-puberulent without; staminal tube ⅓-⅔ the length of the petals, glabrous or puberulent near the top; anthers usually twice as many as the petals, alternating with deltoid lobes which are nearly as long; ovary and style glabrous, the stigma thick-capitate. *Fruit* sphaeroidal, glabrous, smooth before dehiscence, the 3-4 valves transversely striate-rugulose after opening flat or reflexing to expose the 1 or 2 red-arillate seeds.

Forest understory and in fence rows in the West Indies and Mexico to Panama.

CHIRIQUÍ: valley of upper Río Chiriquí Viejo, *White & White 109;* El Boquete, alt. 1,000-1,300 m., *Pittier 3144;* Bajo Choro, *Davidson 347.*

2. TRICHILIA MORITZII C. DC., Monogr. Phaner. **1**: 707. 1878.

Trichilia polyneura C. DC., Bull. Herb. Boiss. ser. 2, **5**: 426. 1905.
Trichilia eurysepala Harms, Notizbl. Bot. Gart. Mus. Berlin **10**: 246. 1928.

Tree to 15 m. tall. *Leaves* to 40 cm. long, paripinnate; leaflets 3-5 pairs borne suboppositely or alternately on the rachis, one leaflet of the apical pair becoming terminal; blades 6-30 cm. long, 2.5-14 cm. wide, elliptical to broadly so, the base acute, the apex short-acuminate, subacute, glabrous to puberulent along the veins above and below. *Inflorescences* axillary, 3-20 cm. long, the axis and branches usually densely velutinous, racemose-paniculate. *Flowers* white or cream, 4-5 mm. long, 4- to 6-merous; sepals and petals deeply imbricate, frequently minutely resinous-dotted; calyx of nearly free sepals, these large, rounded, generally turned and wrinkled in herbarium specimens, velutinous without; corolla velutinous without, glabrous within, the petals obovate; staminal tube ¾ the height of the corolla, sparingly puberulent to puberulent without, the anthers usually twice as many as the petals alternating with apicula nearly as long, the tube sometimes breaking into filaments at the apex and the anther is then subtended by 2 apicula. *Fruit* unknown.

A tree of apparently sporadic occurrence in the Lesser Antilles and ranging from Costa Rica to Peru and Venezuela.

CHIRIQUÍ: Progreso, *Cooper & Slater 194.*

3. Trichilia japurensis C. DC. in Mart., Fl. Bras. **11**(1): 214. 1878.

Moschoxylon pentandrum Poepp. & Endl., Nov. Gen. Sp. Pl. **3**: 39. 1843.
Trichilia Tocachaeana C. DC., Monogr. Phaner. **1**: 701. 1878.
Moschoxylon pachypodum Rusby, Mem. Torrey Bot. Club **6**: 17. 1896.
Trichilia LeCointei Ducke, Archiv. Jard. Bot. Río de Janeiro **3**: 130, 191. 1922.
Trichilia Froesii A. C. Sm., Bull. Torrey Bot. Club **61**: 193. 1934.
Trichilia erythrocarpa Lundell, Bull. Torrey Bot. Club **64**: 551. 1937.
Trichilia Matudae Lundell, Lloydia **2**: 94, *tab.* 5. 1939.
Trichilia pachypoda (Rusby) C. DC. ex Harms in Engl. & Prantl, Nat. Pflanzenf. ed. 2, **19b1**: 114. 1940.

Tree to 25 m. tall. *Leaves* to 40 cm. long; leaflets 4-7 pairs borne alternately on the rachis with one leaflet of the terminal pair oriented in line with the rachis to simulate a terminal leaflet; blades 5-18 cm. long, 2-6 cm. wide, lanceolate-elliptical to obovate, the base acute, sometimes cuneate, the apex acuminate, subacute to acute, glabrous to scattered-puberulent beneath and along the midrib above. *Inflorescences* axillary, racemose-paniculate, 5-25 cm. long, glabrate to usually puberulent over-all. *Flowers* cream, 2-3 mm. long, 4- to 6-merous; calyx cupulate, the margin nearly entire or shallowly lobed, the lobes short-deltoid, scattered-puberulent to pubescent without, glabrous within; corolla scattered-puberulent to pubescent without, glabrous within; staminal tube about ½ the height of the corolla, glabrous or scattered-puberulent without, the anthers usually twice as many as the corolla lobes, alternating with apicula about ⅓ the length of the anthers; ovary pubescent, the stigma thick-capitate. *Fruit* salmon to bright red, elongate, ellipsoidal, the valves 2-3 or 4, very thin, densely short-velutinous frequently with dense patches of longer, lighter trichomes at the base, the calyx frequently persistent; seeds usually solitary in the capsule, arillate.

Wide ranging, lowland species from southern Mexico to the Amazon basin.

BOCAS DEL TORO: Changuinola Valley, Almirante region, *Cooper & Slater 52.* DARIEN: Cana-Cuasi trail, *Davidson 1457;* La Palma, *Pittier 6960;* Marraganti, *R. S. Williams 1015.*

The group of species of *Trichilia* to which *T. japurensis* belongs is much confused. Only a thorough monograph of the genus will finally settle the specific differences between this species and *T. moschata* Sw. as they intergrade completely along the Caribbean coast.

4. Trichilia Cipo (A. Juss.) C. DC. in Mart., Fl. Bras **11**(1): 214. 1878.

Moschoxylum Cipo A. Juss., Mém. Mus. Hist. Nat. Paris **19**: 280. 1830.
Moschoxylum multiflorum Karst., Fl. Columb. **2**: 71, *tab. 136.* 1863.
Trichilia verrucosa C. DC., Monogr. Phaner. **1**: 695. 1878.
Trichilia tuberculata C. DC., loc. cit. 711. 1878.
Trichilia Steinbachii Harms, Notizbl. Bot. Gart. Mus. Berlin **9**: 1156. 1927.

Tree to 25 m. tall. *Leaves* to 30 cm. long; leaflets 3-6 pairs borne alternately on the rachis (rarely oppositely), 1 leaflet of the terminal pair sometimes oriented with the axis to simulate the terminal leaflet of an imparipinnate leaf; blades 4-17 cm. long, 1.5-6.5 cm. wide, lanceolate to elliptical, occasionally somewhat obovate, the base usually acute, the apex obtuse to acuminate-obtuse, the midrib markedly

raised above; leaflets and rachis glabrous, very rarely minutely puberulent. *Inflorescences* axillary, paniculate, 5-20 cm. long, glabrous to scattered-puberulent. *Flowers* white or greenish, 4- to 6-merous, 2-3 mm. long; calyx saucer-shaped, the lobes deltoid, glabrous to pubescent without; petals puberulent or pubescent without, glabrous within; staminal tube ⅔-¾ the height of the corolla, glabrous or scattered-pubescent without; anthers as many as or twice as many as the corolla lobes, alternating with an apiculum ⅓-½ the length of the anthers; ovary and style generally pubescent, the stigma disk-like. *Fruit* red to brown, ellipsoidal, muricate, 3- to 4-valved, with only 1 or 2 seeds developing per fruit; seeds covered with a red aril.

Moist forests at low elevations from Guatemala to Bolivia.

BOCAS DEL TORO: Water Valley, *von Wedel 691*. CANAL ZONE: Gatún Lake, *Bangham 434, 618;* Barro Colorado Island, *Aviles 1141, L. H. & E. Z Bailey 394, Zetek Z-5073* Fort San Lorenzo, *Johnston 1517* CHIRIQUÍ: Progreso, *Cooper & Slater 240;* Puerto Armuelles, alt. 0-75 m., *Woodson & Schery 902;* Comarca del Barú, *Stern & Chambers 146.*

5. TRICHILIA TRIFOLIA L., Syst. Nat. ed. 10, 1020. 1759.

Trichilia Palmeri C. DC., Bot. Gaz. **19**: 39. 1894.
Trichilia unifoliola Blake & Standley, Jour. Wash. Acad. Sci. **15**: 103. 1925.

Shrub or tree to 10 m. tall. *Leaves* 1-1.5 cm. long, 1- or 3-foliate; leaflets 1.5-7 cm. long, 1-4 cm. wide, obovate to elliptical, the base subacute, the apex emarginate to rounded, rarely obtusely short-acuminate, glabrous on both sides, rarely with the rachis, petiolules and principal veins scattered-puberulent. *Inflorescences* axillary, crowded-racemose and appearing to be fascicled, glabrous or scattered puberulent; bracts persistent, deltoid-naviculate. *Flowers* white, 4- to 6-merous, 2-3 mm. long; calyx cupulate, shallowly lobed, the lobes deltoid, glabrous; corolla glabrous; stamens twice as many as the petals, nearly the same height as the corolla, united for the basal ⅓; filaments broad, glabrous without, pilose within, tipped with 2 elongate, deltoid apicula which may nearly hide the anther from without; ovary densely sericeous; stigma sphaeroidal-capitate. *Fruit* an obovoid capsule 0.5-0.75 cm. long, glabrate or scattered pilose, usually 3-valved, 1- to 2-seeded; seeds arillate.

A shrub or small tree of better-drained areas from Mexico to the Caribbean coast of Colombia and Venezuela.

HERRERA: Pese, *Allen 807*. PANAMA: near Río Jagua, *Hunter & Allen 481;* Río Tócumen, *Standley 26685;* Punta Paitilla, *Piper 5426, Standley 26314, 30810;* between Matías Hernández and Juan Díaz, *Standley 31989;* Matías Hernández, *Standley 28881;* Bella Vista, *Standley 25333.*

6. TRICHILIA MONTANA H. B. K., Nov. Gen. Sp. Pl. **7**: 226. 1825.—Fig. 5.

Trichilia excelsa Benth., Hook. Jour. Bot. Kew Gard. Misc. **3**: 368. 1851.
Trichilia macrophylla Benth., loc. cit. 369. 1851.
Trichilia flava C. DC. in Mart., Fl. Bras. **11**(1): 203. *t. 59.* 1878.

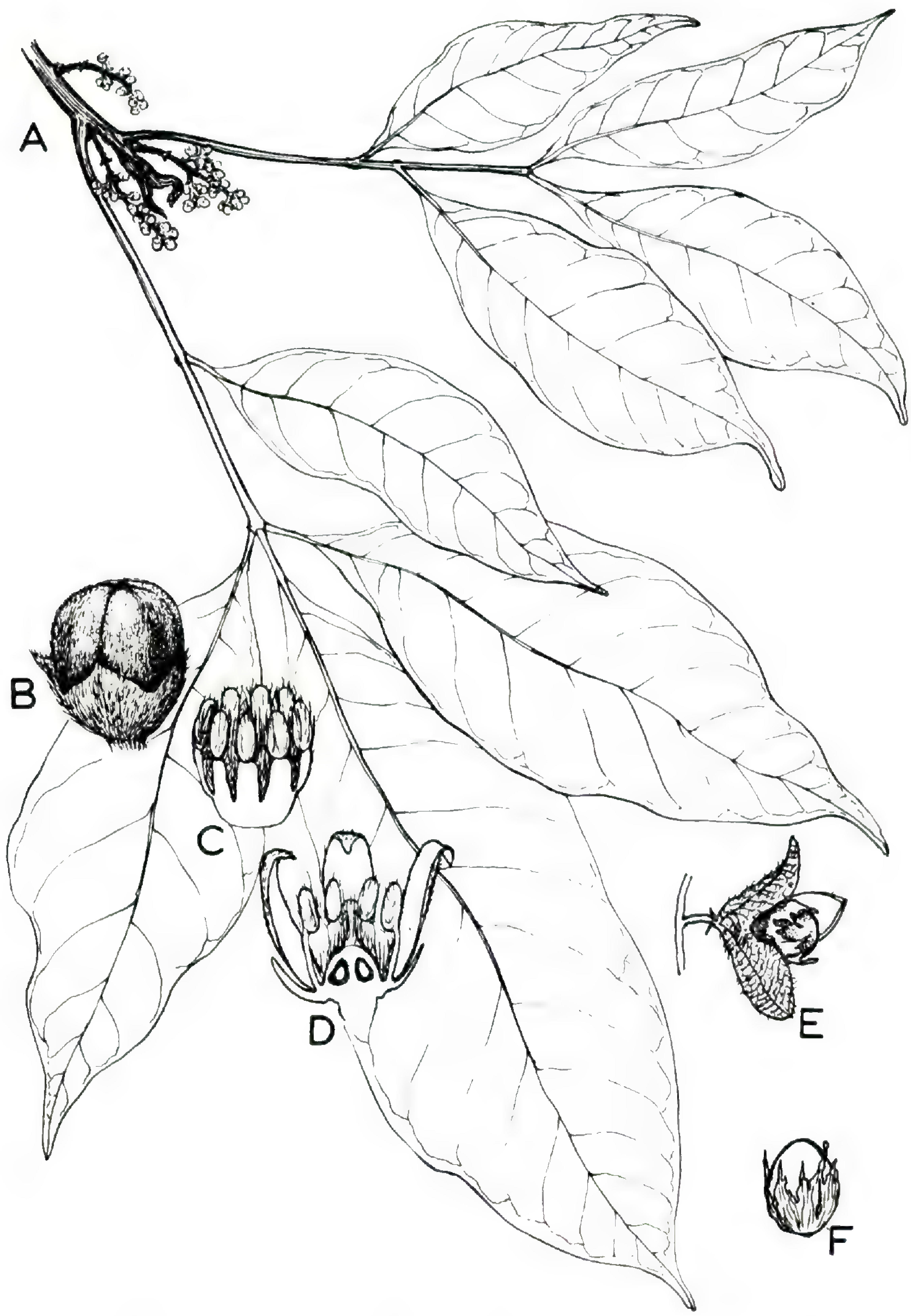

Figure 5. Trichilia montana H. B. K.: A, habit (ca. × 1/2); B, flower bud (ca. × 4); C, androecium (ca. × 4); D, flower, longitudinal section (ca. × 4); E, dehiscing capsule with seed (ca. × 1 1/3); F, seed (ca. × 1 1/3).

Tree to 25 m. tall. *Leaves* to 20 cm. long, imparipinnate; leaflets 2-3 pairs borne oppositely on the rachis and a terminal leaflet; blades 4-32 cm. long, 2-14 cm. wide, usually broadly-elliptical to obovate, occasionally lanceolate-elliptical, the base acute, sometimes cuneate, the apex usually acuminate, subacute, rarely obtuse, glabrous on both sides, lighter in color beneath. *Inflorescences* axillary, racemose-paniculate, sometimes so short as to appear fascicled, infrequently glabrous, generally scattered-puberulent to pubescent, to about 4 cm. long. *Flowers* white, cream or greenish, 3-4 mm. long, 4- to 6-merous; calyx shallow and deeply lobed, the lobes deltoid, glabrous to pubescent without; corolla glabrous to minutely puberulent without and within; staminal tube ⅔ the height of the corolla, united on the basal ½, the filaments glabrous without, pubescent within; anthers twice as many as the petals, pubescent; ovary densely pilose with golden trichomes; stigma sphaeroidal-capitate. *Fruit* ellipsoidal, about 1 cm. long, densely velutinous, sometimes transversely striate, occasionally bearing densely produced epidermal protuberances to about 1 mm. long which are densely velutinous; seeds generally 1 per capsule, arillate.

Moist forests from Mexico to Brasil.

BOCAS DEL TORO: s. loc., *von Wedel 272, 435.* CHIRIQUÍ: San Felix, alt. to 120 m., *Pittier 5196;* vicinity of San Bartolomé, alt. to 50 m., *Woodson & Schery 867;* Progreso, *Cooper & Slater 212, 235.* DARIEN: between Paya and Palo de las Letras, *Stern, Chambers, Dwyer & Ebinger 192;* near mouth of Río Yapé, *Allen 350.*

7. TRICHILIA HIRTA L., Syst. Nat. ed. 10, 1020. 1759.

Trichilia spondiodes Jacq., Enum. Syst. Pl. 20. 1760.
Trichilia Wawrana C. DC., Monogr. Phaner. **1**: 666. 1878.
Trichilia Pringlei Rose, Contr. U. S. Nat. Herb. **8**: 50. 1903.
Trichilia parvifoliola C. DC., Ann. Conserv. Jard. Bot. Genève **10**: 155. 1907.

Tree to 10 m. tall. *Leaves* to 35 cm. long; leaflets 6-9 pairs (occasionally leaves bear a terminal leaflet) borne oppositely on the rachis; blades 3-10 cm. long, 1.5-4 cm. wide, lanceolate-elliptical to ovate, inequilateral and acute at the base, the apex usually narrowly acuminate, glabrous to pubescent along the veins above and below to scattered-pilose all over, the underside often lighter than the top. *Inflorescences* axillary, racemose, numerous toward the ends of the twigs, 6-14 cm. long, glabrous to puberulent. *Flowers* white to lavender, fragrant, 2-3 mm. long, 4- to 6-merous; calyx small, flat, deeply lobed, the lobes deltoid, glabrous to puberulent without; petals lanceolate-ovate to ovate, glabrous; staminal ring united only on the basal ⅓, the filaments glabrous without, pilose within near the apex, bearing a pair of apicula at the base of the anther; stamens usually twice as many as the petals; ovary densely pilose, the stigma sphaeroidal-capitate. *Fruit* about 1 cm. long, reddish, densely short-velutinous, occasionally transversely striate as the valves open, 3- to 4-valved, usually 2- to 4-seeded, the seeds red-arillate and persistent.

Trees of fence rows, forest margins and forests from Mexico to Brasil.

CANAL ZONE: Canal Zone Experimental Garden, *Lindsay 497.* CHIRIQUÍ: vicinity of San Felix, alt. 0-120 m., *Pittier 5140.* PANAMA: Cabuya, *Allen 2557;* between Matías Hernández and Juan Díaz, *Standley 31953;* Las Sabanas, *Standley 25876;* San José Island, *Johnston s. n., 159, 474.*

8. Trichilia tomentosa H. B. K., Nov. Gen. Sp. Pl. **5:** 215. 1822.

Trichilia cuneata Radlk., Sitzungsb. Bayer. Akad. Wiss. Munch., Math.-Phys. Cl. **9:** 642. 1897.
Trichilia Biolleyi C. DC., Bull. Herb. Boiss., ser. 2, **5:** 423. 1905.
Trichilia Biolleyi var. *nicoyensis* C. DC., loc. cit. 424. 1905.
Trichilia acutanthera C. DC., loc. cit. 422. 1905.
Trichilia anisopleura C. DC., loc. cit. 424. 1905.
Trichilia chiriquina C. DC., Smithson. Misc. Coll. **68**(6): 6. 1917.
Trichilia colombiana Cuatr., Field Mus. Nat. Hist., Bot. Ser. **27**(1): 81. 1950.

Tree to 15 m. tall. *Leaves* to 30 cm. long, imparipinnate; leaflets 3 to 4 pairs borne oppositely on the rachis, 3-29 cm. long, 1.5-11 cm. wide, elliptical to obovate, the base subacute to cuneate, the apex acuminate obtuse to subacute, pubescent on both surfaces or pubescent along the nerves only or nearly glabrous. *Inflorescences* axillary, paniculate, sometimes markedly congested, 5-30 cm. long, glabrate to velutinous to short-tomentose. *Flowers* white or cream, 2-3 mm. long, 4- to 6-merous; calyx shallow, deeply deltoid-lobed, glabrate to pubescent without; petals obovate or elliptical, generally minutely velutinous without, glabrate within; stamens twice as many as the petals, united into a shallow cup at the base but free for most of their length, glabrous or glabrate without, bearing a patch of long tomentum at the apex of the filaments within, the filaments truncate or bearing 2 short apicula at either side of the anther; anthers glabrate; ovary densely long-pilose; style short; stigma sphaeroidal-capitate. *Fruit* to about 1.2 cm. long, generally obpyramidal and opening by 2 or 3 valves, orange-yellow or reddish, the valves densely velutinous and transversely striate; seeds usually 1 per capsule, arillate.

A moderate-sized tree of moist forests ranging from southern Mexico to northern Peru.

bocas del toro: Fish Creek Hills, *von Wedel 2434.* chiriquí: vicinity of David, *Pittier 2838;* vicinity of Remedios, *Allen 3477;* Progreso, *Cooper & Slater 214.* panama: Chepo, *Kluge 47;* San José Island, *Johnston 584, 585, 1341.*

6. GUAREA Allemand ex L.

Guarea Allemand ex L., Mant. Pl. 150, 228. 1771, nom. gen. conserv.
Samyda L., Sp. Pl. 443. 1753.
Ruagea Karst., Fl. Columb. **2:** 51, *pl. 126.* 1863.
Sycocarpus Britt., Bull. Torrey Bot. Club **14:** 143. 1887.

Trees or shrubs, the Panamanian species all generally tree-like, but may be shrubby from stump sprouts. *Leaves* pinnate-compound, only rarely with a terminal leaflet, the leaflets opposite or alternate. *Inflorescences* axillary. *Flowers* perfect; calyx saucer to cup-shaped or of 5 nearly distinct sepals; petals 4-6; staminal tube urceolate or cylindric, entire or shallowly lobed, anthers 8-12, included or, rarely, barely exserted; ovary 4- to 12-celled, the ovules 1 or 2 per cell, superposed. *Fruit* a thick or woody-valved capsule loculicidally dehiscent (sometimes tardily so) from the apex; seeds 1 per capsule or 1-2 per locule, more or less arillate, cotyledons fleshy.

As in other genera in the family, the infrageneric taxa are frequently indistinctly separated in *Guarea*. While descriptions for 80 or more species have been published, the number of readily recognizable species is probably less than 35.

a. Ovary glabrous or sparsely pubescent.
  b. Leaflets about 3 times longer than broad; veins generally light in color; capsule to 2 cm. in diam.; seeds entirely covered with a red aril. ....1. G. GLABRA
  bb. Leaflets about twice as long as broad; veins generally dark in color; capsule to 4 cm. in diam.; seeds only about 4/5 covered by a red aril. ....2. G. KUNTHIANA
aa. Ovary densely pubescent or sericeous.
  c. Inflorescence glabrate or only sparingly pubescent; calyx shallowly cupulate, frequently deeply lobed; capsule globose to fig-shaped, usually lenticellate, about 1.5 cm. in diam. ....3. G. GUIDONIA
  cc. Inflorescence sparsely to densely pubescent; calyx deeply cupulate, usually shallowly lobed; capsules elenticellate.
    d. Leaflets pubescent along the veins above and below, frequently villose over the entire under surface of the blade; capsule globose, often densely velutinous, to 2.5 cm. in diam. ....4. G. TONDUZII
    dd. Leaflets only puberulent on the veins above and below or glabrous, the blades sometimes scattered papillose; capsule fig-shaped, pulverulent, to 3 cm. in diam. and 3 cm. long. ....5. G. MULTIFLORA

1. GUAREA GLABRA Vahl, Eclog. Am. **3:** 8. 1807.

Guarea Swartzii DC., Prodr. **1:** 624. 1824.
Guarea excelsa H. B. K., Nov. Gen. Sp. Pl. **7:** 227. 1825.
Guarea Schomburgkii C. DC., Monogr. Phaner. **1:** 565. 1878.
Guarea Donnell-Smithii C. DC., Bull. Herb. Boiss., ser. 2, **5:** 419. 1905.
Guarea syringoides C. H. Wright, Kew Bull. 1906: 3. 1906.
Guarea Rovirosae C. DC., Ann. Conserv. Jard. Bot. Genève **10:** 145. 1907.
Guarea brevianthera C. DC., Smithson. Misc. Coll. **68**(6): 1. 1917.
Guarea ternifoliola C. DC., loc. cit. 2. 1917.
Guarea parva C. DC., loc. cit. 3. 1917.
Guarea racemiformis Blake, Contr. U. S. Nat. Herb. **20:** 241. 1919.
Guarea heterophylla Blake, Proc. Biol. Soc. Wash. **34:** 116. 1921.
Guarea polyantha Blake, loc. cit. 117. 1921.
Guarea chiricana Standley, Trop. Woods **16:** 18. 1928, nom. nud.; Field Mus. Nat. Hist., Bot. Ser. **4:** 215. 1929.

Tree to 20 m. tall, frequently shorter. *Leaves* approximately 20-40 cm. long; leaflets 2-6 (-10) pairs, lanceolate-elliptical to elliptical, rarely broadly ovate-elliptical, the base generally acute, the apex obtuse to acuminate-obtuse, glabrous to puberulous along the midrib above, glabrous to puberulous to scattered-pilose along the veins beneath (the specimens from the northern Antilles and north and west of Nicaragua on the mainland generally barbate in the axils of the veins beneath). *Inflorescences* shorter than the leaves, 3-20 or more cm. long, generally paniculate, less frequently nearly racemose, puberulent to pubescent. *Flowers* greenish-white to cream or pink, 4- to 5-(-6)-merous; calyx shallowly to definitely cupulate, the divisions often apiculate, glabrous to puberulous, the apicula frequently pubescent; petals spatulate, glabrous to completely puberulent without, usually with a lighter margin; staminal tube entire to obscurely lobed, rarely scattered-puberulent without; anthers 8-10 (-12); ovary glabrous to scattered-hirsute, borne on a narrow gynophore. *Capsule* red, glabrous, usually 4-valved, the largest seen about 2 cm. in

diam., nearly globose, sometimes obscurely 4-sided, 4-seeded; seeds apparently always entirely covered by a red aril.

A medium-sized tree of broad distribution in the forests of the West Indies, Mexico to Colombia, Ecuador and Venezuela and, perhaps, to Bolivia.

CANAL ZONE: Barro Colorado Island, *Zetek 15001;* Río Indio de Gatún, *Pittier 2810.* CHIRIQUÍ Remedios and vicinity, alt. 0-100 m., *Pittier 5466;* Progreso, *Cooper & Slater 164, 168, 212, 229, 250.* DARIEN: headwaters of the Río Chico, alt. 500-750 ft., *Allen 4625;* vicinity El Real, Río Tuira, *Stern, Chambers, Dwyer & Ebinger 111;* vicinity of Paya, Río Paya, *Stern, Chambers, Dwyer & Ebinger 182.*

2. Guarea Kunthiana A. Juss., Mèm. Mus. Hist. Nat. Paris **19:** 290. 1830.

Guarea Poeppigii Tr. & Pl., Ann. Sci. Nat., Bot., ser. 5, **15:** 371. 1872.
Guarea erythrocarpa C. DC., Bull. Herb. Boiss., ser. 2, **5:** 420. 1905.
Guarea Caoba C. DC., loc. cit. 421. 1905.
Guarea Cook-Griggsii C. DC., Smithson. Misc. Coll. **68**(6): 2. 1917.
Guarea Williamsii C. DC., loc. cit. 4. 1917.
Guarea Steinbachii Harms, Notizbl. Bot. Gart. Mus. Berlin **10:** 348. 1928.
Guarea Matudai Lundell, Lloydia **2:** 93. 1939.
Guarea macrantha Standley & Williams, Ceiba **1:** 240. 1951.

Tree to about 25 m. tall, frequently shrubby at higher elevations in Central America. *Leaves* approximately 18-40 cm. long; leaflets 2-3(-5) pairs, broadly elliptical, occasionally broadly obovate, the base obtuse to acute, the apex obtuse to obtusely long-acuminate, the veins frequently darker than the blade beneath, glabrous above and beneath, rarely minutely puberulent along the veins beneath. *Inflorescences* shorter than the leaves (rarely elongate in specimens from the upper Amazon drainage), often cauliflorous, 3-18 cm. long (in specimens seen from Panama), paniculate, rarely nearly racemose, glabrous, infrequently minutely puberulent. *Flowers* white or cream, sometimes tinged with rose, 4 (rarely 5)-merous; calyx cupulate, frequently split at one side, the lobes rounded to very short minutely puberulent without; staminal tube usually entire, glabrous; anthers 8 (-10); ovary glabrous, borne on a thick gynophore. *Capsule* dull red, glabrous, usually 4-valved, the largest capsule seen about 4 cm. in diam., usually definitely 4-lobed, shorter than broad, sometimes lenticellate, 4-celled, with 1 or 2 seeds per cell; seeds $4/5$ covered by a red aril, the remaining $1/5$ covered by a white caruncle on the axial side.

Apparently nearly restricted to the lowland forest from southern Mexico to Bolivia.

CANAL ZONE: west of Limon Bay, Río Piña-Río Media divide, *Johnston 1700.* CHIRIQUÍ: Bajo Chorro, Boquete District, alt. 6,000 ft., *Davidson 46.* DARIEN: trail between Paya and Palo de las Letras. *Stern, Chambers, Dwyer & Ebinger 213;* Boca de Cupe, *R. S. Williams* 683.

3. Guarea guidonia (L.) Sleumer, Taxon **5:** 194. 1956.—Fig. 6.

Samyda guidonia L., Sp. Pl. 443. 1753.
Melia Guara Jacq., Enum. Syst. Pl. 20. 1760.
Trichilia Guara (Jacq.) L., Sp. Pl. ed. 2, 551. 1762.
Guarea Guara (Jacq.) P. Wilson, N. Am. Fl. **25:** 272. 1924.

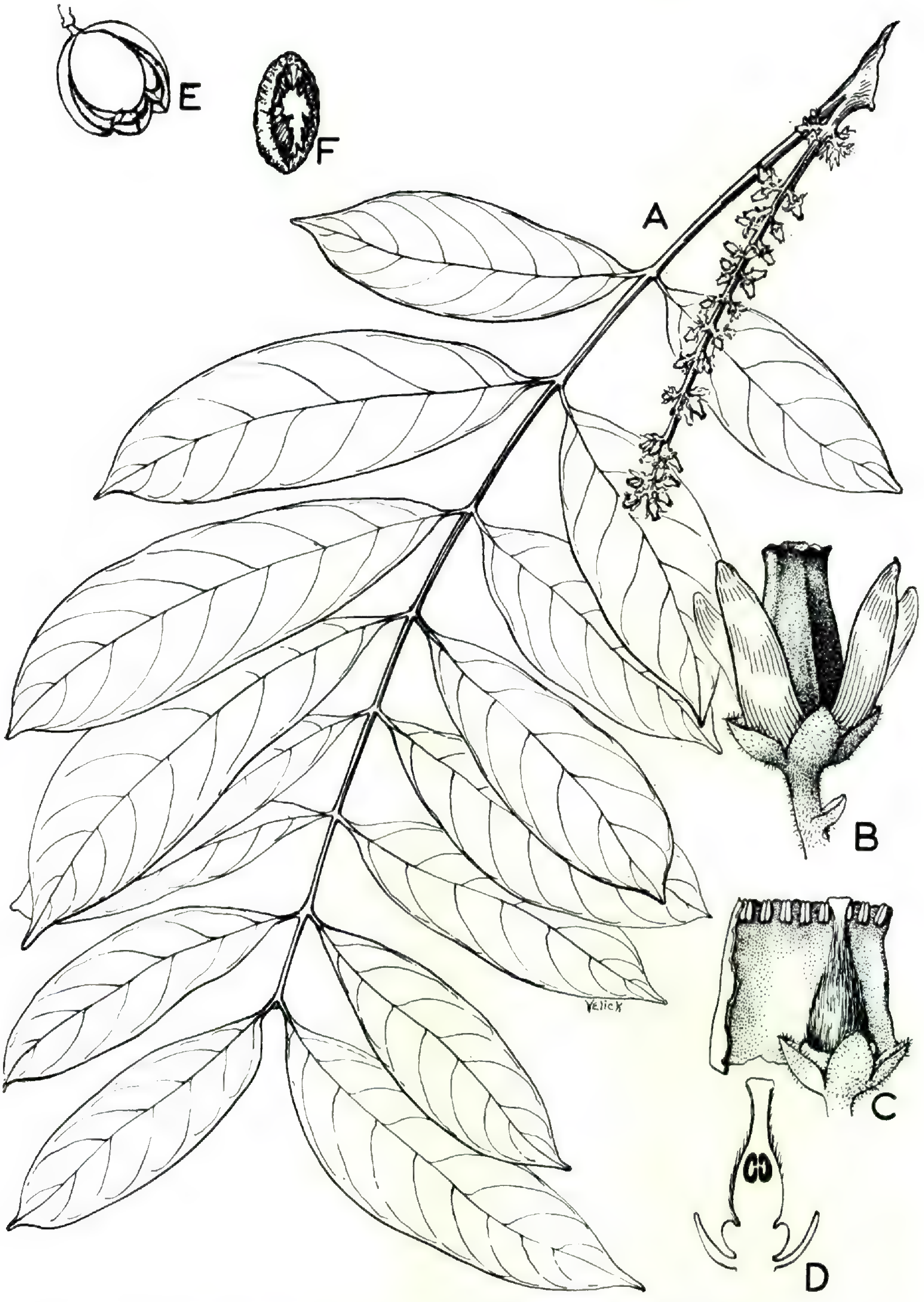

Figure 6. GUAREA GUIDONIA (L.) Sleumer: A, habit (ca. × ½); B, flower (ca. × 4); C, id., petals removed, the staminal tube opened (ca. × 4); D, longitudinal section of the gynoecium (ca. × 4); E, dehiscing capsule (ca. × ½); F, seed (ca. × 1).

Guarea trichilioides L., Mant. Pl. 228. 1771.
Guarea trichilioides var. *brachystachya* C. DC., Monogr. Phaner. **1:** 544. 1878.
Guarea trichilioides var. *pallida* C. DC., loc. cit. 544. 1878.
Guarea trichilioides var. *pachycarpa* C. DC., loc. cit. 544. 1878.
Guarea trichiloides var. *colombiana* C. DC., Ann. Conserv. Jard. Bot. Genève **10:** 138. 1907.
Guarea trichiloides var. *decandra* C. DC., loc. cit. 139. 1907.
Guarea rubra C. DC., Monogr. Phaner. **1:** 556. 1878.
Guarea Langsdorffiana C. DC., loc. cit. 557. 1878.
Guarea subspicata C. DC., Ann. Conserv. Jard. Bot. Genève **10:** 143. 1907.
Guarea puberula Pittier, Bol. Soc. Venez. Cienc. Nat. **4:** 357. 1938.

Tree to 25 m. tall, sometimes shrubby. *Leaves* 10-50 cm. long; leaflets 4-7 pairs (occasionally there is a terminal leaflet), elliptical or lance-elliptical, rarely broadly elliptical, the base subacute to acute, the apex obtuse to acuminate-subacute, glabrous to puberulent along the veins above and below, the rachis glabrous, the blade rarely minutely scattered-papillose. *Inflorescences* axillary, 4-35 cm. long, paniculate, frequently strict, glabrate to sparsely pubescent. *Flowers* white to yellow, rarely pink, 4- to 5-merous; calyx shallowly cupulate, shallowly to deeply lobed, lobes rounded to deltoid, occasionally apiculate, glabrate to puberulent particularly on the apiculum; petals scattered-puberulous to densely puberulent without, glabrous to puberulent within; staminal tube nearly entire to crenulate to deltoid-dentate, glabrous; anthers 8 (-10); ovary sparingly to densely pubescent, borne on a glabrous gynophore. *Capsule* light to dark-rufous-brown, frequently lenticellate, globose to fig-shaped, nitid-glabrous to pulverulent, 4(-5)-valved, 4(-5)-celled, the cells 1-seeded; seeds about ¾ covered by a red aril; the largest capsule seen about 1.5 cm. in diam.

Widely distributed in the American tropics.

CANAL ZONE: along Quebrada Morito, *Johnston 1578, 1634;* mouth of Río Chagres, *Johnston 1772;* Arraiján, *Woodson, Allen & Seibert 780;* Barro Colorado Island, *Woodworth & Vestal 747;* Gatuncillo, *Piper 5626.* CHIRIQUÍ: Boquete District, Bajo Choro, *Davidson 712.* DARIEN: Boca de Cupe, *R. S. Williams 685;* Marraganti, *R. S. Williams 633.* PANAMA: Río Tócumen, *Standley 29343, 29352.*

While this species has long been known as *Guarea trichilioides* through much of its range and as *G. Guara* in Panama, Sleumer (loc. cit. 1956) pointed out the existence of an earlier name for the species in another genus. This name is based on interpretations of Plumier's descriptions of 1703 in *Nova Plantarum Americanum genera,* and the description and plate in the Burmann edition of Plumier's work, *Plantarum Americanarum,* of 1755-60 and the intervening and subsequent history of use by other authors. Urban had identified the plate in 1920 as *G. trichilioides* but had not made the nomenclatural transfers required by priority. There can be no doubt about the identity of the plant illustrated.

Since the correct identification of the plate also provides an earlier name for the genus *Guarea,* Sleumer proposed the conservation of the generic name *Guarea* Allemand ex L. over the generic name *Samyda* L. but the Committee for Spermatophyta Conservation of Generic Names felt that this was unnecessary as *Samyda* L. is automatically rejected under the present wording of the Code (Regnum Vegetabile **23:** Art. 14, Note 3. 1961) (See, Taxon **9:** 15. 1960).

4. Guarea Tonduzii C. DC., Smithson. Misc. Coll. **68**(6): 4. 1917.

Tree generally less than 15 m. tall. *Leaves* about 5-45 cm. long, leaflets 2-3 (-5) pairs, broadly ovate-elliptical to elliptical, the base obtuse to acute, the apex usually acuminate, obtuse, the blade usually densely pubescent along the veins above, villous over the entire under surface, rarely pubescent along the veins only, with scattered pubescence on the blade beneath. *Inflorescences* shorter than the leaves, cauliflorous, 6-16 cm. long, paniculate, densely pubescent. *Flowers* light-cream to pinkish-tan, 4-merous; calyx cupulate, split on one side, the lobes rounded, densely pubescent, rarely sparsely pubescent; petals spatulate, densely pubescent, rarely sparsely pubescent without, glabrous within; staminal tube slightly crenulate, sparsely pubescent to glabrous without; anthers 8; ovary densely pubescent, rarely sparsely pubescent or glabrous, borne on a thick, glabrous gynophore. *Capsule* red to reddish-brown, oblate-sphaeroidal, densely velutinous to glabrous, 4-valved, occasionally with 1 seed per locule, frequently only with 1 seed developing per fruit; the largest fruit seen about 2.5 cm. in diam.; seeds apparently entirely covered by a red aril.

Costa Rica and Panama.

CANAL ZONE: Barro Colorado Island, *Carpenter 71.* CHIRIQUÍ: vicinity of Boquete, alt. 5,500 ft., *Stern, Chambers, Dwyer & Ebinger 1090.* DARIEN: trail between Paya and Pucro, *Stern, Chambers, Dwyer & Ebinger 398.*

5. Guarea multiflora A. Juss., Mém. Mus. Hist. Nat. Paris **19**: 284. 1830.

Sycocarpus Rusbyi Britt., Bull. Torrey Bot. Club **14**: 143. 1887.
Guarea Rusbyi (Britt.) Rusby, Mem. Torrey Bot. Club **6**: 17. 1896.
Guarea culebrana C. DC., Smithson. Misc. Coll. **68**(6): 5. 1917.
Guarea longipetiola C. DC., loc. cit. 5. 1917.
Guarea Pittieri C. DC., loc. cit. 6. 1917.
Guarea fissicalyx Harms, Notizbl. Bot. Gart. Mus. Berlin **11**: 383. 1932.
Guarea Mancharra Cuatr., Field Mus. Nat. Hist., Bot. Ser. **27**(1): 71. 1950.

Tree to 50 m. tall, frequently flowering when only 6-10 m. tall, occasionally shrubby (sprout clumps?). *Leaves* 0.15-2 m. long; leaflets 4-17 pairs, elliptical to lanceolate-elliptical, rarely ovate or subovate, the base subacute to rounded, the apex subacute to obtuse, frequently acuminate obtuse, glabrous or puberulent along the veins above and below, then the petiolules and the rachis puberulent, sometimes scattered papillose on the blade. *Inflorescences* generally axillary, 8-35 cm. long, paniculate, sparsely to densely puberulent. *Flowers* white or yellow, 4- to 6-merous; calyx frequently reddish or orange, cupulate, split on one side, the lobes rounded, sometimes apiculate, glabrate to puberulent or pubescent; petals densely puberulent to sericeous without, glabrous within; staminal tube entire to somewhat crenulate, glabrous or sparingly puberulent without; anthers 8-12; ovary densely pubescent, borne on a thick, glabrous gynophore. *Capsule* apparently rufous-brown, fig-shaped, pulverulent, 4- to 6-valved, 4- to 6-celled; generally 1, sometimes 2 seeds developing per cell; the largest fruit seen about 3 cm. long and 3 cm. in diam.;

seeds about 7/8 covered by a red aril, about 1/8 showing a soft, white caruncular growth.

Frequent in lowland forest from southern Mexico to Bolivia.

BOCAS DEL TORO: Cocoa Cay, *von Wedel 2874;* Changuinola Valley, *Dunlap 506.* CHIRIQUÍ: Progreso, *Cooper & Slater 208;* vicinity of San Bartolomé, *Woodson & Schery 923.* COLÓN: Río Culebra above Sta. Isabel, *Pittier 4160.* DARIEN: near Garachiní, *Pittier 5697;* Boca de Pauarandó, Sambú River, *Pittier 5580.* PANAMA: San José Island, *Erlanson 488, Johnston 1, 645.*

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FLORA OF PANAMA[1]

Part VI

Family 104. HIPPOCRATEACEAE[2]

By Calaway H. Dodson[3] and André Robyns[3, 4]

Lianas, shrubs or sometimes trees; milky latex present or not. *Leaves* usually opposite, occasionally subopposite or alternate, simple, petiolate, generally stipulate, the stipules interpetiolar, small, caducous, sometimes absent. *Inflorescences* axillary or terminal, sometimes extra-axillary, thyrsoid, cymose, racemose, paniculate or fasciculate, sometimes flowers solitary. *Flowers* bracteolate, usually small, hermaphrodite, infrequently unisexual, antinomorphous; calyx usually almost divided to the base, the lobes generally 5, infrequently 2-4, imbricate, equal or not, usually persistent; petals mostly 5 (3-4), imbricate or valvate, entire to serrate at the margins; disc generally present, various, often conspicuous, usually continuous, rarely discontinuous; stamens usually 3, inserted usually within the disc, the filaments free or often connate basally; anthers basifixed, 2-thecate, the thecae distinct or more or less confluent, extrorse or introrse, dehiscing transversely or longitudinally; pollen grains simple or in tetrads; ovary superior, often concealed within the disc and sometimes adnate to it, (2-) 3-celled, the placentation axile, the ovules 2-many in each cell, usually collateral or 2-seriate, anatropous; style 1, usually short, rarely none, the stigmas obscure or obvious, usually 3, entire or bifid. *Fruits* of 3 capsular mericarps, these attached separately to the receptacle or connate proximally, dehiscing along a median, longitudinal suture and 2-valvate, or drupaceous or baccate; seeds few to numerous, with a more or less developed, basal wing or wingless and imbedded in mucilaginous pulp, exalbuminous; cotyledons free or united.

A family of 18 genera, chiefly distributed in the tropics of both hemispheres. The 12 genera recognized by A. C. Smith in his comprehensive work on the American *Hippocrateaceae* (Brittonia **3:** 341-555, *12 figs.* 1940) occur in Panama.

The *Hippocrateaceae* are very closely related to the *Celastraceae* and are often treated as a part of the latter.

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[1] The Flora of Panama by Robert E. Woodson, Jr. and Robert W. Schery and Collaborators should be cited as: Ann. Missouri Bot. Gard., with volume number, pagination and date of the Annals.

[2] Assisted by National Science Foundation Grants No. G-7144 to the first author (Principal Investigator, R. E. Woodson, Jr.) and GB-170 to the second author (Principal Investigator, H. C. Cutler).

[3] The co-authors have adapted this article from "The American Species of *Hippocrateaceae*" by A. C. Smith, Brittonia **3:** 341-555. 1940.

[4] I wish to express my sincere thanks and appreciation to the curators of the following herbaria for the facilities for study: Chicago Natural History Museum and United States National Herbarium, Washington, D. C.

a. Fruit drupaceous; seeds wingless, embedded in mucilaginous pulp.
  b. Disc discontinuous, composed of 3 saccate, staminiferous lips; anthers dehiscing transversely; style 0 .... 1. CHEILOCLINIUM
  bb. Disc continuous; style present.
    c. Disc short-cylindric, membranous or thin-carnose.
      d. Flowers 4.5-5 mm. in diam.; anthers dehiscing by transversal, confluent clefts; fruit up to 11 cm. in diam. .... 2. TONTELEA
      dd. Flowers 1.7-2.2 mm. in diam.; anthers dehiscing by longitudinal clefts, the connective obvious; fruit up to 3 cm. long and about 1 cm. in diam. .... 3. PERITASSA
    cc. Disc annular-pulvinate, carnose .... 4. SALACIA
aa. Fruit composed of 3 capsular mericarps; seeds with a more or less developed, basal wing; disc continuous; anthers dehiscing transversely.
  e. Mericarps connate proximally; flowers (5.5-)7-11 mm. in diam.
    f. Petals serrate at the margins; disc short-cylindric, carnose; ovules 8-14 per cell, imbricate in a mass; flowers 10-11 mm. in diam. .... 5. ANTHODON
    ff. Petals entire and often revolute at the margins; disc annular-pulvinate, thick-carnose; ovules 6-8 per cell, 2-seriate; flowers (5.5-)7-10 mm. in diam. .... 6. HEMIANGIUM
  ee. Mericarps attached separately to the receptacle.
    g. Disc short-cylindric, membranous to carnose.
      h. Flowers 1.5-2.7 mm. in diam.
        i. Sepals as long as broad, acute or subacute; pericarp woody; flowers 1.5-2 mm. in diam. .... 7. HYLENAEA
        ii. Sepals broader than long, rounded; pericarp thin-coriaceous; flowers 2-2.7 mm. in diam. .... 8. ELACHYPTERA
      hh. Flowers 10-17 mm. in diam.; sepals broader than long, rounded; pericarp thin-coriaceous .... 9. CUERVEA
    gg. Disc annular-pulvinate, conspicuously carnose.
      j. Leaf-blades scabrous; disc conspicuously flattened and puberulus; flowers 9-12 mm. in diam. .... 10. PRIONOSTEMMA
      jj. Leaf-blades not scabrous; disc not both flattened and puberulus; flowers 1.7-8 mm. in diam.
        k. Flowers 1.7-3.5 mm. in diam.; petals glabrous; disc minute, forming an annular cushion below the stamens, glabrous .... 11. PRISTIMERA
        kk. Flowers 4-8 mm. in diam.; petals barbellate within; disc conspicuous, cupuliform, minutely tomentellous-papillate without .... 12. HIPPOCRATEA

1. CHEILOCLINIUM Miers*

CHEILOCLINIUM Miers, Trans. Linn. Soc. London **28:** 420. 1872.

Lianas or slender shrubs or trees usually with the upper branches scandent, glabrous throughout or essentially so, the branches and branchlets opposite; milky latex present. *Leaves* opposite, petiolate. *Inflorescences* axillary, pedunculate, thyrsoid, corymbose or cymose. *Flowers* hermaphrodite, small, pedicellate; sepals 5, narrowly imbricate, semiorbicular to deltoid or ovate, often erosulous or fimbriolate at the margins; petals 5, narrowly imbricate, usually rounded at the apex and entire, often thinly carnose; disc discontinuous, composed of 3 saccate, carnose, staminiferous lips confluent with the base of the ovary; stamens 3, the filaments often slightly enlarged at the apex, the anthers small, extrorsely nutant, transversely ellipsoid, dehiscing by transversal, confluent, extrorse clefts; ovary 3-lobed,

* The reader may refer to Smith (Brittonia **3:** 341-555. 1940) for complete generic and specific synonymy.—Editor.

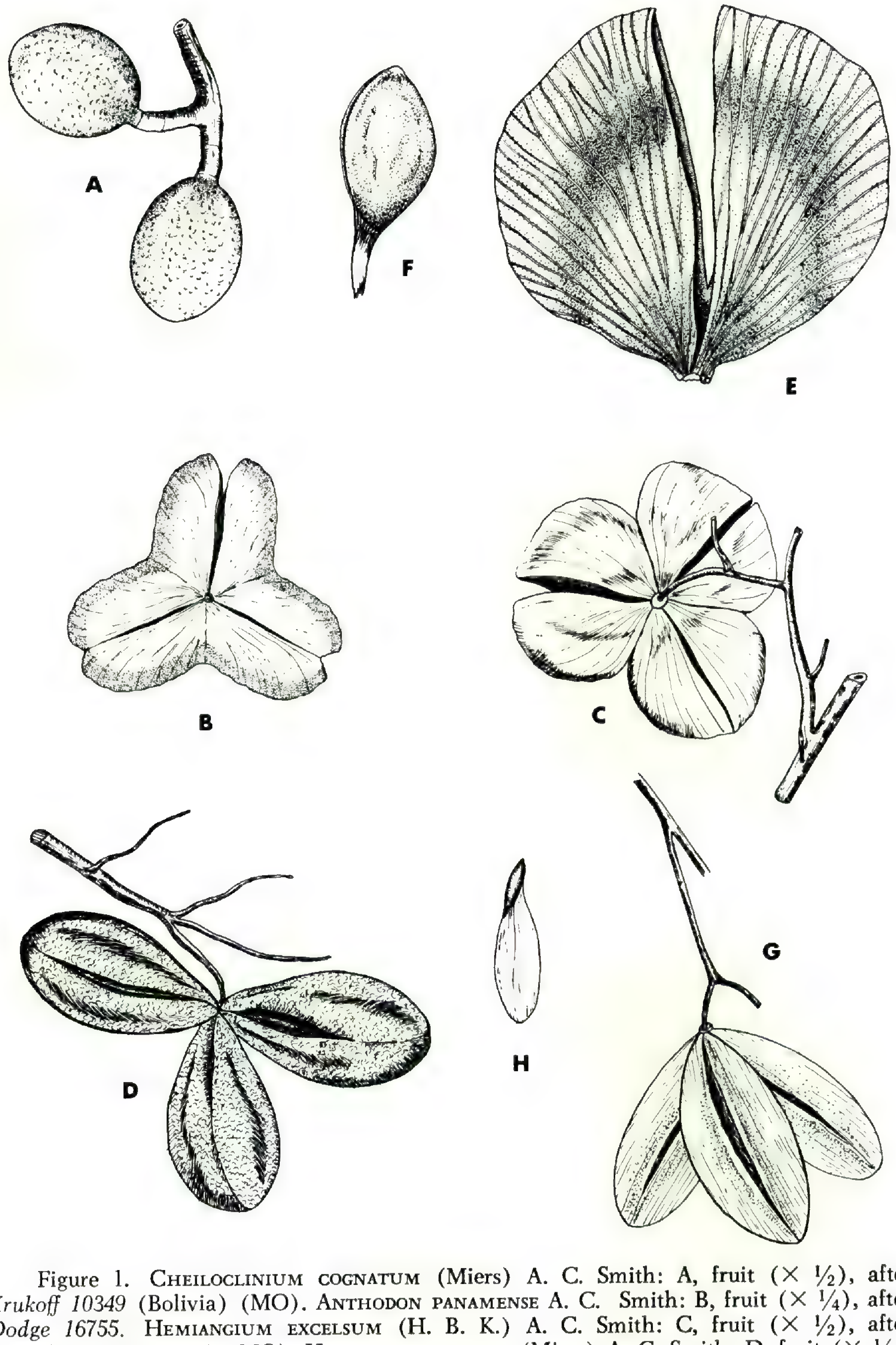

Figure 1. CHEILOCLINIUM COGNATUM (Miers) A. C. Smith: A, fruit (× ½), after *Krukoff 10349* (Bolivia) (MO). ANTHODON PANAMENSE A. C. Smith: B, fruit (× ¼), after *Dodge 16755*. HEMIANGIUM EXCELSUM (H. B. K.) A. C. Smith: C, fruit (× ½), after *Matuda 4788* (Mexico) (MO). HYLENAEA PRAECELSA (Miers) A. C. Smith: D. fruit (× ¼), after *Stern, Chambers, Dwyer & Ebinger 942*. CUERVEA KAPPLERIANA (Miq.) A. C. Smith: E, mericarp (× ½), F, seed (× ½), after *Stern, Chambers, Dwyer & Ebinger 965*. HIPPOCRATEA VOLUBILIS L.: G, fruit (× ½), H, seed (× ½), after *Dodge, Steyermark & Allen 16825*.

flattened at the truncate apex, 3-celled, the cells 2- or 4-ovulate, the ovules usually attached to the upper portion of the interior angles, collateral or superposed or in superposed pairs; stigmas 3, sessile, radiating, entire or emarginate or bilobed, opposite the stamens and alternating with the cells of the ovary. *Fruits* drupaceous, small or medium-sized, subglobose, the pericarp coriaceous, the dissepiments soon evanescent; seeds 2-6, embedded in mucilaginous pulp, angulate, wingless.

A neotropical genus of 20 species, of which only one has been encountered in Panama.

1. CHEILOCLINIUM COGNATUM (Miers) A. C. Smith, Brittonia **3:** 529. 1940.—Fig. 1(A).

Kippistia cognata Miers, Trans. Linn. Soc. London **28:** 417. 1872.

Shrub or slender tree up to 12 m. high, the branches often scandent. *Leaves* with the blade oblong or elliptic-oblong or ovate-oblong, obtuse or subacute at the base, acuminate at the apex, narrowly revolute and subentire or crenate at the margins, 8-20 cm. long and 2.5-8 cm. broad, chartaceous, the costa prominent on both sides. *Inflorescences* short-pedunculate, thyrsoid, 2-10 cm. long. *Flowers* congested in ultimate dichotomies or paired at the end of ultimate branchlets, the pedicel stout, very short and usually less than 1 mm. long; sepals broadly deltoid-ovate or semiorbicular, obtuse at the apex, entire or faintly erosulous at the margins, 0.7-1.3 mm. long; petals 5, suberect, oblong or obovate-oblong, rounded at the apex, entire at the margins, 1.5-2.6 mm. long, subcarnose or subcoriaceous, opaque or obscurely lineolate; lips of the disc 0.3-0.4 mm. high; filaments of the stamens ligulate, 0.4-0.7 mm. long, the anthers about 0.2 mm. long and 0.3 mm. broad; ovary 1-1.3 mm. in diam., the ovules 2 per cell and collateral, the stigmas linear and obtuse. *Fruits* spherical or oblong-ellipsoid, up to 3.5 cm. long and 3 cm. broad, the pericarp 1-2 mm. thick, obscurely rugulose, often lenticellate; seeds few, 4-6, often superposed in pairs, ovate, up to 15 mm. long.

Panama to Amazonian Peru and Bolivia and to Rio de Janeiro; West Indies (Tobago).

CANAL ZONE: below Gatun, banks of the Chagres River, *Maxon 4796!* (F, US). DARIEN: Marraganti, *R. S. Williams 1005!* (NY, US). PANAMA: Cerro Azul, *Dwyer 1395!* (US).

In *Dwyer 1935,* the leaves and the fruits, although immature, are smaller than in the typical *C. cognatum.*

2. TONTELEA Aubl.

TONTELEA Aubl., Hist. Pl. Gui. Fr. 31. 1775.

Lianas or slender shrubs or trees with the upper branches scandent, glabrous throughout or essentially so; milky latex often present. *Leaves* opposite or subopposite, rarely alternate, petiolate, the petiole canaliculate. *Inflorescences* axillary or arising from defoliate branchlets, pedunculate or not, thyrsoid-paniculate or

pseudodichotomously branching. *Flowers* hermaphrodite, small, sessile or short-pedicellate, arranged in loose clusters of 2-5 near or at the apex of ultimate branchlets; sepals 5, narrowly imbricate, broader than long, obtuse or rounded at the apex, entire to fimbriate at the margins; petals 5, narrowly imbricate, usually rounded at the apex, entire to erosulous at the margins, submembranous to thin-carnose; disc continuous, short-cylindric, free or sometimes adnate to the ovary by inconspicuous, interstaminal septa, entire or undulate or crenulate at the margin, membranous to thin-carnose; stamens 3, rarely 4, erect to subspreading, the filaments ligulate, the anthers usually extrorsely nutant, broader than long, the thecae usually subglobose and laterally confluent, dehiscing by transversal, confluent, extrorse clefts; ovary depressed-conical or 3-gonous, the angles usually rounded, 3-celled, each cell usually 2-ovulate, the ovules collateral or superposed; style short, terete, carnose, the stigmas 3, obvious and divaricate, alternate with or opposite to the stamens and the cells of the ovary, entire or 2-lobed, sometimes obscure. *Fruits* drupaceous, often large, the pericarp coriaceous or woody, the dissepiments persistent or evanescent; seeds usually few, embedded in mucilaginous pulp, angulate, wingless.

A neotropical genus of 31 species, one of which occurs in Panama.

1. TONTELEA RICHARDII (Peyritsch) A. C. Smith, Brittonia **3:** 478. 1940.

Salacia Richardi Peyritsch in Mart., Fl. Bras. **11**(1): 148. 1878.

Liana, the branches stout, subterete. *Leaves* opposite, the petioles stout, 12-17 mm. long, the blade elliptic to oblong, rounded or obtuse and decurrent at the base, cuspidate or short-acuminate at the apex, entire and slightly recurved at the margins, 9-20 cm. long and 4-10 cm. broad, coriaceous or thin-coriaceous, the costa stout and prominent on both surfaces. *Inflorescences* axillary, thyrsoid-paniculate or pseudocymose, 3-4.5 cm. long. *Flowers* 4.5-5 mm. in diam.; sepals semiorbicular, rounded at the apex, entire, 0.7-1.3 mm. long and 1-1.5 mm. broad, papyraceous; petals elliptic- or subspatulate-obovate, 1.7-2.5 mm. long and 1.3-2.2 mm. broad, thin-carnose; disc erect, subentire or undulate at the margin, 0.3 mm. high, submembranous; stamens erect, the filaments 0.4-0.6 mm. long, slightly expanded toward the base, the anthers 0.3-0.5 mm. long and 0.6-0.9 mm. broad; ovary trigonous-conical, the style 2 per cell, superposed; style 0.2-0.4 mm. long, the stigmas spreading, deltoid, alternate with the stamens. *Fruits* often paired, subglobose or somewhat obovoid, slightly contracted at the base, rounded at the apex, up to 11 cm. in diam., the pericarp woody, finely rugulose without, the dissepiments persistent and coriaceous; seeds few, oblong-ovoid, 3-4 cm. long.

Panama and the Guianas; a colloquial name in Panama is *bejuco de canjura.*

CANAL ZONE: Barro Colorado Island, *Aviles 54!* (F), *Shattuck 658!* (F, MO), *Wetmore, Abbe & Shattuck 92!* (F), *Zetek 3823!* (F).

3. PERITASSA Miers

Peritassa Miers, Trans. Linn. Soc. London **28:** 402. 1872.

Lianas, shrubs or slender trees with the upper branches scandent, glabrous throughout or nearly so. *Leaves* opposite, subopposite or alternate, petiolate, the petiole canaliculate. *Inflorescences* axillary or arising from defoliate branchlets, pedunculate, thyrsoid-paniculate, corymbose or cymose. *Flowers* hermaphrodite, small, subsessile or shortly pedicellate, congested or loosely arranged toward the apex of ultimate branchlets; sepals 5, narrowly imbricate, suborbicular to deltoid, erosulous or fimbriolate at the margins; petals 5, narrowly imbricate, rounded at the apex, usually erosulous at the margins, thin-carnose or submembranous; disc continuous, erect or suberect, short-cylindric, free, often crenulate at the margin, membranous to thin-carnose; stamens 3, usually erect, the filaments ligulate, the anthers extrorse, the thecae vertical or oblique, dorsally adnate to a thickened connective and laterally contiguous, dehiscing by longitudinal clefts, the connective sometimes produced into an apiculum; ovary usually depressed-subglobose, 3-celled, each cell 2- or 4-ovulate, the ovules collateral or somewhat superposed, attached to the interior angles near the center, sometimes one erect and the other suspended; style short, tapering, truncate, the stigmas obscure. *Fruits* drupaceous, small or medium-sized, the pericarp chartaceous to woody, the dissepiments soon evanescent; seeds 2-6, imbedded in mucilaginous pulp, angulate, wingless.

A neotropical genus of 14 species, one of which occurs in Panama.

1. Peritassa pruinosa (Seem.) A. C. Smith, Brittonia **3:** 520. 1940.

Salacia pruinosa Seem., Bot. Voy. Herald 90. 1853; Hemsl. (sub *Hippocratea sp.* 10), Biol. Centr.-Am. **1:** 194. 1880.

Sicyomorpha pruinosa Miers, Trans. Linn. Soc. London **28:** 411. 1872.

Liana or shrub with scandent branches, the branchlets slender, cinereous, copiously lenticellate. *Leaves* opposite or subopposite, the petiole stout, 6-12 mm. long, rugose; blade elliptic or obovate-oblong, obtuse at the base, obtusely short-cuspidate at the apex, entire or obsoletely crenulate at the margins, 10-20 cm. long and 3.5-9.5 cm. broad, thin-coriaceous, the costa prominent on both surfaces. *Inflorescences* compactly dichotomously several times branched, 1-2.5 cm. long, the peduncle short. *Flowers* usually paired or ternate, 1.7-2.2 mm. in diam., the pedicel slender and about 1 mm. long; sepals ovate-deltoid, rounded at the apex, erosulous to densely ciliate at the margins, 0.4-0.6 mm. long and slightly broader, papyraceous; petals oblong, erosulous or minutely ciliolate distally, 1-1.3 mm. long and 0.7 mm. broad, papyraceous or thin-carnose; disc subentire at the margin, about 0.2 m. high, thin-carnose or submembranous; filaments of the stamens about 0.6 mm. long, the thecae distinct, slightly divergent at the base, about 0.2 mm. long, dehiscing by longitudinal, oblique clefts, the connective deltoid; ovary about 0.5

mm. in diam., the ovules 2 per cell, the style about 0.3 mm. long, the stigmas obscure or minutely capitate. *Fruits* 1 per inflorescence, subcylindric-ellipsoid, sometimes falcate, up to 3 cm. long and about 1 cm. in diam., the pericarp woody, at least 2 mm. thick; seeds 1-2.

Panama and northern Colombia.

PANAMA: Hacienda de Tapia, *Seemann 1219* (K, type; photo F, US); near Panama, *Hayes 652* (K).

4. SALACIA L.

SALACIA L., Mant. Pl. 159. 1771.

Lianas, scandent or sometimes erect shrubs, rarely slender trees with the upper branches scandent, glabrous throughout or essentially so, the branchlets usually terete, the bark smooth or lenticellate; milky latex sometimes present. *Leaves* opposite or alternate, the petiole canaliculate, stipulate or not, the stipules small and soon deciduous. *Inflorescences* axillary or on defoliate branchlets, cymose, paniculate, racemose or fasciculate. *Flowers* hermaphrodite, rarely unisexual by abortion, often relatively large for the family, pedicellate, congested or loosely arranged; calyx usually deeply 5-lobed, the lobes unequal, frequently scarious and erosulous at the margins; petals usually 5, imbricate, sessile or sometimes subunguiculate, entire or erosulous at the margins; disc continuous, annular-pulvinate, truncate-conical or flattened, carnose; stamens usually 3, suberect to reflexed, the filaments ligulate, usually broadened toward the base, the anthers dehiscing by a transversal, apical or extrorse cleft, or by 2 longitudinal or oblique and mostly apically confluent clefts; pollen grains simple; ovary usually immersed in the disc, conical, cylindric or 3-lobed, (2-)3-celled, the cells 2- to many-ovulate, the ovules collateral, superposed or in superposed pairs; ovary gradually narrowed into a distinct or obscure style, the stigmas obscure. *Fruits* drupaceous, subglobose or ellipsoid, the pericarp coriaceous, 1- to 3-celled, the dissepiments evanescent or not; seeds 1-many, embedded in mucilaginous pulp, wingless; cotyledons massive, free or united.

A pantropical genus of about 200 species. A. C. Smith (Brittonia **3:** 423-463. 1940) lists 29 species from the Western Hemisphere; only one imperfectly known species occurs in Panama.

1. SALACIA MEGISTOPHYLLA Standley, Field Mus. Nat. Hist., Bot. Ser. **4:** 222. 1929; A. C. Smith, Brittonia **3:** 439. 1940.

Liana, the branchlets stout, lenticellate. *Leaves* opposite, the petiole stout, 1.8-2 cm. long, strongly rugose; blade ovate-oblong, rounded at the base, obtusely and gradually short-acuminate at the apex, entire and narrowly revolute at the margins, the costa sharply elevated above, prominent beneath, 34-37 cm. long and 13-14 cm. wide, thick-coriaceous, rugose on both surfaces. *Flowers* unknown. *Fruits* more or less globose, up to 5-6 cm. in diam., the pericarp coriaceous, 2-3 mm. thick, minutely rugulose, the fruiting pedicel woody, 6-9 mm. in diam.; seeds apparently 2-4, probably about 3 cm. long.

Panama and Venezuela.

BOCAS DEL TORO: Region of Almirante, Cricamola, *Cooper 503!* (F, type).

An additional collection, *Ch. & W. von Hagen 2133!* (MO, NY) (Chiriquí, Boquete region, Cerro Horqueta), can possibly be referred to this species. Indeed, the shape, texture and venation of the leaves, and the fruits strongly suggest *S. megistophylla,* but both the leaves and the fruits are too small.

5. ANTHODON Ruiz & Pavon

Anthodon Ruiz & Pavon, Fl. Peruv. Chil. **1:** 45. 1798.

Lianas, the branches stout, terete, cinereous, the branchlets usually opposite, elongate, slender. *Leaves* opposite or subopposite, petiolate. *Inflorescences* axillary, pedunculate, cymose, dichotomously branched. *Flowers* hermaphrodite, paired or ternate at the apex of ultimate inflorescence-branchlets or solitary in distal dichotomies, pedicellate; sepals 5, erosulous or ciliolate at the margins; petals 5, imbricate, spreading, serrate at the margins; disc continuous, suberect, short-cylindric, usually flattened or grooved on the margin, carnose; stamens 3, suberect, the filaments ligulate, the anthers broadly reniform, dehiscing by apical, transversal, confluent clefts; ovary depressed-3-lobed, 3-celled, the cells 8- to 14-ovulate, the ovules imbricate in a mass attached to the inner basal angle; style stout, carnose, the stigmas 3, minute, often obscure, opposite the stamens. *Fruits* of 3 flattened, capsular mericarps, these spreading, firmly connate proximally, convex on both surfaces, sharp and entire at the margin, inconspicuously carinate and dehiscing along a median suture, the pericarp coriaceous, flabellate-costate without, smooth within; seeds 8-14 per mericarp, closely imbricate, affixed by a basal, membranous wing.

A neotropical genus of two species, one from Panama.

1. Anthodon panamense A. C. Smith, Brittonia **3:** 422, *fig.* 8 (*a-f*). 1940.—Fig. 1(B).

Hippocratea malpighiaefolia sensu Standley, Contr. Arnold Arb. **5:** 93. 1933, pro parte quoad *Woodworth & Vestal 715,* non Rudge (1805).

Liana, glabrous throughout, the branchlets subterete or faintly quadrangular, cinereous or brownish. *Leaves* with the petiole 5-8 mm. long, the blade elliptic or elliptic-oblong, obtuse at the base, obtuse or obtusely short-cuspidate at the apex, undulate or crenulate at the margins, 8-11 cm. long and 3-5.5 cm. broad, papyraceous, the costa elevated or nearly plane above, prominent beneath. *Inflorescences* 2.5-5 cm. long. *Flowers* 10-11 mm. in diam., the bracteoles ovate; sepals semiorbicular, rounded at the apex, erosulous at the margins, 1.3-1.5 mm. long and 2.2 mm. broad, papyraceous; petals elliptic-oblong or ovate-lanceolate, rounded at the apex, conspicuously serrate at the margins, 5-5.5 mm. long and 2.5-3 mm. broad, carnose; disc entire at the margin and flattened or rounded at the apex, about 0.5 mm. high; filaments of the stamens slightly broadened toward the base, 0.8-1 mm. long, the anthers about 0.6 mm. long and 1-1.2 mm. broad; ovary about 1 mm. in diam., the style about 0.5 mm. long. *Fruits* up to 15 cm. in diam., the mericarps connate for 3-5 cm., broadly oblong-deltoid, often conspicuously emarginate at the apex,

the pericarp about 0.2 mm. thick distally and 0.5 mm. thick toward the base; seeds 10-14 per mericarp.

Native to Panama; a local name is *bejuco de estrella.*

CANAL ZONE: Barro Colorado Island, *Aviles 56!* (F), *922!* (F), *L. H. & Ethel Zoe Bailey 485!* (F), *Shattuck 922!* (MO), *Woodworth & Vestal 715!* (F). COLÓN: along trail to triangulation station on top of Tumba Vieja, 90-400 m., *Dodge 16755!* (MO); along Río Sirrí, Trinidad Bassin, 20-50 m., *Pittier 4018!* (F, type).

6. HEMIANGIUM A. C. Smith

HEMIANGIUM A. C. Smith, Brittonia **3:** 411. 1940.

Lianas or erect, woody plants, the branches stout, terete, glabrous, the branchlets opposite, sparsely lenticellate. *Leaves* generally opposite, petiolate. *Inflorescences* axillary or rarely crowded in groups of 4-6 at the apex of short, leafless branchlets, pedunculate, paniculate or pseudocymose. *Flowers* hermaphrodite, rather large for the family, pedicellate, loosely arranged, usually solitary at the apex of ultimate branchlets; sepals 5; petals 5, suberect or spreading, glabrous; disc continuous, annular-pulvinate, conspicuous, slightly narrowed and entire at the margin, thick-carnose, glabrous; stamens 3, suberect or spreading, the filaments ligulate, conspicuously broadened and nearly contiguous at the base, the anthers transversely ellipsoid, the thecae laterally confluent, dehiscing by apical, transversal, confluent clefts; ovary more or less immersed in the disc, depressed-3-lobed, 3-celled, the cells 6- to 8-ovulate, the ovules 2-seriate; style subulate, the stigmas obscure. *Fruits* few per inflorescence, of 3 capsular mericarps, these spreading, connate at the basal margins, slightly convex on both surfaces, emarginate at the apex, bluntly carinate and dehiscing along a median suture, the pericarp coriaceous; seeds 6-8 par mericarp, affixed by a basal wing, the embryoniferous portion coriaceous, the wing membranous.

A monotypic, neotropical genus.

1. HEMIANGIUM EXCELSUM (H. B. K.) A. C. Smith, Brittonia **3:** 414, *fig.* 7. 1940. —Fig. 1(C).

Hippocratea excelsa H. B. K., Nov. Gen. Sp. Pl. **5:** 139. 1822; Benth., Bot. Voy. Sulphur 78. 1844; Miers, Trans. Linn. Soc. London **28:** 340. 1872; Hemsl., Biol. Centr.-Am. **1:** 193. 1880.

Liana or shrub or slender tree up to 10 m. high, the young parts often puberulus or tomentellous. *Leaves* with the petiole slender, 5-10 mm. long, canaliculate; blade oblong-elliptic or obovate or narrowly so, narrowly rounded or subattenuate at the base, rounded, obtuse, cuspidate or rarely callose-mucronate at the apex, obsoletely crenulate or crenate-serrate and often narrowly revolute at the margins, 3-14 cm. long and 3-7.5 cm. wide, chartaceous or thin-coriaceous, sometimes persistently tomentellous beneath. *Inflorescences* 1.5-6 cm. long, the peduncle often slightly flattened, 1-2.5 cm. long, the branchlets terete. *Flowers* (5.5-)7-10 mm. in diam., the pedicel about 3-5 mm. long, puberulus or glabrous, the bracteoles

2-3, about 0.5 mm. long; sepals deltoid-ovate or suborbicular, subacute to rounded at the apex, entire or erosulous and often scarious at the margins, 0.9-1.5 mm. long and 0.9-2(2.8) mm. broad, submembranous to thin-carnose, often puberulus without, sometimes glandular-punctate or -lineolate; petals oblong, elliptic-oblong or ovate-elliptic, rounded or obtuse at the apex, entire and often narrowly revolute at the margins, 3-5 mm. long and 2-4 mm. broad, submembranous or thin-carnose, sometimes glandular; disc 0.5-1.3 mm. high; filaments of the stamens 0.8-1.8 mm. long, the anthers 0.3-0.6 mm. long and 0.7-1.1 mm. broad; ovary 1-1.3 mm. in diam., the style 0.5-1.5 mm. long. *Mericarps* connate proximally for 0.8-3 cm., attached to a swollen receptacle, elliptic or broadly obovate, sharp and entire at the margins, 4-6 cm. long and 3.5-6.5 cm. wide, the pericarp inconspicuously flabellate-costate without, smooth within; seeds with the embryoniferous portion ovoid, 7-10 mm. long and 3-7 mm. broad, the wing obovate-elliptic, slightly falcate, up to 3.5 cm. long and 1.5 cm. wide.

From southern Mexico to Colombia and Venezuela, also in southeastern Brazil and Paraguay.

VERAGUAS: locality unknown, *Hinds s. n.* (fide Benth., loc. cit.; Miers, loc. cit.; and Hemsl., loc. cit.).

7. HYLENAEA Miers

HYLENAEA Miers, Trans. Linn. Soc. London **28:** 366. 1872.

Lianas or slender trees with scandent branches, glabrous throughout. *Leaves* opposite or subopposite, petiolate, the petioles shallowly canaliculate. *Inflorescences* axillary, pedunculate, much branched, paniculate-corymbose or pseudocymose, the branchlets slender or not. *Flowers* hermaphrodite, minute, pedicellate; sepals 5, usually longer than broad or as long as broad, acute or subacute, membranous; petals 5, imbricate, faintly erosulous at the margins, membranous; disc continuous, erect, short-cylindric, membranous to thin-carnose; stamens 3, suberect or reflexed, the filaments ligulate, gradually broadened toward the base, the anthers extrorsely nutant, subglobose or transversely oblong, dehiscing by apical, transversal, confluent clefts; ovary depressed-3-lobed, 3-celled, each cell 4- or 6-ovulate the ovules 2-seriate, ascending from the inner basal angle; style carnose, the stigmas obscure. *Fruits* of 3 capsular mericarps, these divergent, separately attached to a greatly swollen receptacle, conspicuously convex on both surfaces, rounded and blunt at the margins, dehiscing along an obscure median suture, the pericarp woody; seeds 4-6 per mericarp, affixed by a comparatively small, basal wing.

A neotropical genus of two species, one native to Panama.

1. HYLENAEA PRAECELSA (Miers) A. C. Smith, Brittonia **3:** 410, *fig.* 6 *(a-n)*. 1940; Johnston, Sargentia **8:** 188. 1949.—Fig. 1 (D).

Tyloderma praecelsa Miers, Trans. Linn. Soc. London **28:** 414. 1872.
Salacia praecelsa (Miers) Standley, Contr. U. S. Nat. Herb. **27:** 243. 1928.

Liana, the branchlets slender, subterete or distally faintly quadrangular, cinereous or brownish. *Leaves* with the blade elliptic-oblong, rounded or subcordate at

the base, abruptly acuminate or cuspidate at the apex, entire and minutely recurved at the margins, 8-26 cm. long and 3.5-11 cm. broad, chartaceous or thin-coriaceous, lustrous above, the costa prominent on both surfaces. *Inflorescences* 1.5-5 cm. long, the peduncle, rachis and branchlets slender, straight, flattened or quadrangular. *Flowers* 1.5-2 mm. in diam., the pedicel capillaceous, 1.2-1.8 mm. long; sepals oblong-ovate, subacute, obscurely erosulous at the margins, 0.3-0.5 mm. long and broad; petals suberect or spreading, oblong-obovate, rounded at the apex, 1 mm. long and 0.6 mm. broad; disc entire or faintly crenulate at the margin, about 1 mm. high, membranous; stamens suberect, 0.3-0.4 mm. long; ovary 0.3-0-4 mm. in diam., the ovules 4 per cell, the style about 0.2 mm. long. *Mericarps* obovate, rounded or faintly emarginate at the apex, 7.5-10 cm. long, 4-8 cm. broad and 1-2 cm. thick, dehiscing along an obscure median suture and often strongly involute at the sutures at maturity, the pericarp 1.5-2 mm. thick, rugose and conspicuously sparsely furfuraceous without, smooth or flabellate-costate within; seeds 4 or fewer (by abortion) per mericarp, the embryoniferous portion ellipsoid or oblong-cylindric, slightly falcate, 5-6 cm. long and about 1.5 cm. broad, the wing obdeltoid, about 2 cm. long and conspicuously narrowed toward the base.

Native to Panama; one of the local names is *colmillo de puerco*.

CANAL ZONE: near Chargres, *Hayes 708* (K, type; photo F, US); vicinity of Fort Sherman, wooded swamp, *Standley 31107!* (US); along road south of Fort Sherman, *Johnston 1580!* (MO); along the Chagres River below Gatun, near sea level, *Pittier 2805!* (F, US); region of Chagres River, *Babbitt 491!* (F); forest along the Río Indio de Gatun, near sea level, *Pittier 2770!* (US); Barro Colorado Island, *Bangham 523!* (F), *Wetmore & Woodworth 851!* (F). DARIEN: vicinity of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern, Chambers, Dwyer & Ebinger 942!* (MO, US). PANAMA: San José Island, *Johnston 1220!* (MO, US).

8. ELACHYPTERA A. C. Smith

ELACHYPTERA A. C. Smith, Brittonia **3:** 383. 1940.

Lianas or slender trees with scandent branches, glabrous throughout or nearly so, the branches terete. *Leaves* opposite or subopposite, petiolate, stipulate. *Inflorescences* axillary or terminal, many-flowered, paniculate-corymbose, copiously branched, the peduncle and branchlets quadrangular. *Flowers* hermaphrodite, very small, pedicellate; sepals 5, usually broader than long, rounded at the apex; petals 5, imbricate, suberect, entire to erosulous at the margins, thin-carnose; disc continuous, erect, inconspicuous, short-cylindric, often thickened at the margin, carnose or thin-carnose; stamens 3, suberect, the filaments ligulate, the anthers extrorsely nutant, transversely ellipsoid, dehiscing by apical, transversal clefts; pollen grains simple; ovary 3-lobed, 3-celled, each cell 2- or 4- ovulate, the ovules collateral or in superposed pairs, ascending from the inner basal angle; style short, the stigma capitate or 3-lobed, the lobes inconspicuous and opposite the stamens. *Fruits* of 3 capsular mericarps (2 mericarps often abortive), these divergent, separately attached to a slightly swollen receptacle, short-stipitate, nearly flattened or slightly convex on both surfaces, dehiscing along an inconspicuous median suture, the pericarp papyraceous or thin-coriaceous; seeds 1-4 per mericarp, affixed by a very short basal

wing, the wing papyraceous or thin-coriaceous, extended distally into a flange (sometimes greatly expanded) along the inner margin of the embryoniferous portion; cotyledons united.

A genus of tropical America and tropical Africa, consisting of five species; three species are recognized in tropical America, one of which occurs in Panama.

1. Elachyptera floribunda (Benth.) A. C. Smith, Brittonia **3:** 387, *fig.* 3(*a-n*). 1940; Johnston, Sargentia **8:** 188. 1949.

Hippocratea floribunda Benth., Bot. Voy. Sulph. 78. 1844.

Hippocratea celastroides sensu Woodson & Schery, Ann. Missouri Bot. Gard. **29:** 357. 1942, non H. B. K. (1822).

Liana or slender tree with scandent branches. *Leaves* with the petiole 3-9 mm. long, the blade ovate-elliptic or elliptic, acute to rounded at the base, gradually short-acuminate or cuspidate at the apex, entire or crenulate-undulate at the margins, 5-12 cm. long and 2-5 cm. broad, chartaceous, the costa prominent on both surfaces. *Inflorescences* solitary or aggregated in clusters of 2-4, 2-11 cm. long. *Flowers* 2-2.7 mm. in diam., often minutely cinereous-puberulus on all exterior surfaces; sepals deltoid to semiorbicular, subentire or erosulous at the margins, 0.3-0.5 mm. long and 0.4-0.7 mm. broad, submembranous or papyraceous; petals oblong to elliptic, entire or distally erosulous, 1-1.7 mm. long and 0.6-1 mm. broad; disc undulate and slightly thickened at the margin, 0.12-0.2 mm. high; filaments of the stamens 0.3-0.4 mm. long, slightly broadened at base and apex, the anthers about 0.2 mm. long and 0.4 mm. broad; ovary 0.4-0.5 mm. in diam., the ovules 2 per cell, collateral; style 0.1-0.3 mm. long, the stigmas forming a minute, capitate shield, obtuse or faintly emarginate, often obscure. *Fruits* often 5-10 per inflorescence, the mericarps elliptic or slightly obovate, obtuse or rounded or faintly emarginate at the apex, 3-4.5 cm. long, 2-2.5 cm. broad and about 3 mm. thick, the pericarp thin-coriaceous, conspicuously flabellate-costate without, smooth within; seeds 2 per mericarp, the embryoniferous portion ellipsoid, the wing oblong, 4-5 mm. long and 2-3 mm. broad distally, gradually narrowed toward the base, extended distally into a narrow, thickened flange.

Guatemala to Panama and northern South America to Brazil.

bocas del toro: vicinity of Chiriquí Lagoon, Old Bank Island, *von Wedel 2038!* (MO, US). canal zone: south of Fort Sherman, *Johnston 1763!* (MO). chiriquí: Palo Alto, just east of Boquete, alt. 5,000 ft., partly disturbed forest of cloud-forest type, *Stern, Chambers, Dwyer & Ebinger 1011!* (MO, US). colón: Río Indio de Fató, near sea level, *Pittier 4274!* (US). panama: San José Island, *Erlanson 393!* (US), *523!* (US), *562!* (US), *Johnston 484!* (MO, US), *1128 1159*. veraguas: Isla de Coiba (Penal Colony), *Dwyer 2402!* (MO).

9. CUERVEA (Benth. & Hook. f.) Triana ex Miers

Cuervea (Benth. & Hook. f.) Triana ex Miers, Trans. Linn. Soc. London **28:** 370. 1872.

Lianas or shrubs or slender trees with eventually scandent branches, glabrous throughout, the branches terete. *Leaves* opposite or subopposite, petiolate, stipulate.

Inflorescences axillary or aggregated at the apex of branchlets or arranged on short, leafless branchlets, paniculate-corymbose, the flowers loosely arranged and comparatively few per inflorescence, the peduncle and branchlets terete. *Flowers* hermaphrodite, rather large for the family, pedicellate; sepals 5, broader than long, rounded at the apex, membranous; petals 5, imbricate, spreading or suberect, membranous; disc continuous, erect or suberect, short-cylindric, entire or minutely crenulate at the margin, membranous to thin-coriaceous; stamens 3, suberect, the filaments ligulate, conspicuously broadened toward the base, the anthers extrorsely nutant, transversely ellipsoid, dehiscing by apical, transversal, confluent clefts; pollen grains simple; ovary depressed-3-lobed, 3-celled, each cell 4- or 6-ovulate, the ovules 2-seriate, ascending from the inner basal angle; style carnose, the stigmas 3, sometimes conspicuous. *Fruits* of 3 capsular mericarps, these divergent, separately attached to a swollen receptacle, depressed obovoid or suborbicular, abruptly stipitate, rounded or faintly emarginate at the apex, conspicuously convex on both surfaces, dehiscing along an inconspicuous median suture and bivalved, the pericarp thin-coriaceous or papyraceous, flabellate-costate without, smooth or minutely rugulose within; seeds 2-6 per mericarp, thick, obovoid or ellipsoid, affixed by a basal wing, the wing oblong, gradually narrowed toward the base and distally extended into a narrow flange along the inner margin of the embryoniferous portion; cotyledons massive and united.

A genus of four species, three in tropical America and one in tropical Africa; one species occurs in Panama.

1. Cuervea Kappleriana (Miq.) A. C. Smith, Brittonia **3:** 399. 1940.—Fig. 1(E, F).

Hippocratea Kappleriana Miq., Linnaea **26:** 220. 1853.
Cuervea latifolia Miers, Trans. Linn. Soc. London **28:** 372. 1872.
Hippocratea integrifolia sensu Seem., Bot. Voy. Herald 90. 1853, non A. Rich. (1843); Hemsl., Biol. Centr.-Am. **1:** 193. 1880.

Liana, the branchlets usually opposite, often rugose, cinereous or brownish. *Leaves* with the petiole 8-15 mm. long, the blade elliptic-oblong or ovate-oblong, subattenuate and decurrent at the base, gradually acuminate at the apex, entire or obscurely crenulate at the margins, 8-19 cm. long and 4-10 cm. broad, chartaceous, the costa prominent on both surfaces. *Inflorescences* 5-12 cm. long. *Flowers* 10-17 mm. in diam.; sepals broadly ovate or ovate-deltoid, subentire or faintly erosulous at the margins, 1.3-2.5 mm. long, usually obviously flabellate-nerved; petals often strongly concave, obovate-elliptic, rounded at the apex, entire or faintly undulate-crenulate and often inflexed at the margins, 5.5-9 mm. long and 3.5-7.5 mm. broad; disc 0.4-0.7 mm. high, membranous; stamens 1.6-2.2 mm. long; ovary 0.8-1.5 mm. in diam., the ovules 4-6 per cell, the style stout, the stigmas conspicuous, spreading, oblong, obtuse. *Mericarps* depressed-obovate to suborbicular, 5-9 cm. long, 5.5-10 cm. broad and 1-1.5 cm. thick, the pericarp thin-coriaceous; seeds 4-6 per mericarp, the embryoniferous portion 2-5 cm. long and 1.5-3 cm. broad, the wing about 20-25 mm. long and 5-10 mm. broad distally, coriaceous.

Costa Rica, Panama, northern South America and the West Indies.

BOCAS DEL TORO: region of Almirante, *Cooper 474!* (F). DARIEN: vicinity of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa near Quebrada Felix, *Stern, Chambers, Dwyer & Ebinger 965!* (MO, US). VERAGUAS: Isla de Coiba, mouth of Río Juncal, *Dwyer 1651!* (MO, US), *Seemann 643* (K, type of *C. latifolia*).

10. PRIONOSTEMMA Miers

PRIONOSTEMMA Miers, Trans. Linn. Soc. London **28:** 354. 1872.

Lianas, the branches and branchlets opposite or alternate, subterete, sparsely lenticellate. *Leaves* opposite, petiolate, the blade scabrous. *Inflorescences* axillary toward the apex of branchlets, pedunculate, paniculate or pseudocymose; fruiting inflorescences greatly enlarged. *Flowers* hermaphrodite, loosely arranged toward the apex of ultimate branchlets, comparatively large for the family, pedicellate; sepals 5, essentially deltoid, often accrescent; petals 5, unguiculate; disc annular-pulvinate, conspicuously flattened, carnose, puberulus except near the entire margin; stamens 3, inserted at the junction of the disc and the ovary, usually spreading, the filaments ligulate, slightly broadened at the base, the anthers transversely ellipsoid, the thecae subglobose and laterally confluent, dehiscing by apical, transversal, confluent clefts; ovary immersed in the disc, depressed and sharply trigonous, conspicuously puberulus, 3-celled, each cell 8- to 10-ovulate, the ovules 2-seriate; style subulate, obtuse, carnose, the stigmas obscure. *Fruits* few per inflorescence, of 3 capsular mericarps, these divergent, separately attached to a swollen receptacle, obovate or obdeltoid, slightly convex on both surfaces, rounded at margins, bluntly carinate and dehiscing along a median suture, the pericarp coriaceous; seeds 8-10 per mericarp, affixed by a well-developed, membranous, basal wing.

A neotropical, monotypic genus.

1. PRIONOSTEMMA ASPERA (Lam.) Miers, Trans. Linn. Soc. London **28:** 355. 1872; A. C. Smith, Brittonia **3:** 393, *fig. 4.* 1940.

Hippocratea aspera Lam., Tab. Encycl. Méth. **1:** 101. 1791.
Hippocratea malpighiaefolia Rudge, Pl. Gui. 10. 1805; Standley, Contr. Arnold Arb. **5:** 93. 1933, pro parte quoad *Woodworth & Vestal 580.*

Liana with stout branches and slender branchlets, often setulose when young, at length glabrous, usually obscurely scabrous. *Leaves* with the petiole subterete, flattened above, 4-10 mm. long, usually glabrous, scabrous; blade ovate-oblong or elliptic-oblong, rounded or subcordate at the base, bluntly short-acuminate or cuspidate at the apex, entire and often narrowly revolute at the margins, about 7-14 cm. long and 4-7 cm. broad, chartaceous or thin-coriaceous, minutely papillose and scabrous on both surfaces, the costa sharply elevated above, prominent beneath. *Inflorescences* 4-10 cm. long. *Flowers* 9-12 mm. in diam., the pedicel slender, 3-7 mm. long; sepals subacute to rounded at the apex, irregularly erosulous at the margins, 1.7-3 mm. long and broad, thin-coriaceous or carnose, minutely and closely puberulus; petals broadly spatulate, unguiculate, rounded at the apex, deeply and irregularly pectinate-erose at the margins, 4-5 mm. long and broad, membranous, minutely and closely puberulus; disc about 0.5 mm. thick; filaments of the stamens

2.5-3 mm. long, the anthers 0.5-0.6 mm. long and 0.8-1.3 mm. broad; ovary about 1.5 mm. in diam., the style 1.3-2 mm. long. *Mericarps* obtuse and swollen at the base, rounded, truncate, obtuse or slightly emarginate at the apex, 5.5-8 cm. long and 4-6 cm. broad, the pericarp asperate and conspicuously flabellate-costate without, smooth within; seeds with the embryoniferous portion ovoid, up to 14 mm. long and 8 mm. broad, the wing elliptic or obovate, slightly falcate, up to 6 cm. long and 3 cm. broad.

Panama and northern South America, also in subandean Bolivia; Trinidad.

CANAL ZONE: Barro Colorado Island, *Woodworth & Vestal 580!* (F).

11. PRISTIMERA Miers

PRISTIMERA Miers, Trans. Linn. Soc. London **28:** 360. 1872.

Lianas or slender shrubs or trees with scandent branches, glabrous throughout, the branches and branchlets usually opposite, sometimes alternate, slender, lenticellate. *Leaves* opposite, petiolate, the petiole canaliculate. *Inflorescences* axillary or arising from branchlets below the leaves, solitary or aggregated, usually many-flowered, pedunculate, paniculate-corymbose or pseudocymose. *Flowers* hermaphrodite, in distal dichotomies or congested in clusters of 2-5 at the apex of ultimate branchlets, small, pedicellate; sepals 5, rounded or obtuse at the apex; petals 5, spreading or suberect, rounded at the apex, submembranous or thin-carnose; disc minute, forming an annular cushion below the stamens, slightly projecting, often hardly distinguishable from the ovary, carnose; stamens 3, suberect to spreading, the filaments membranous, the anthers extrorsely nutant, transversely ellipsoid, dehiscing by apical, transversal, confluent clefts; ovary depressed-3-lobed, 3-celled, the cells 2- to 8-ovulate, the ovules collateral or in superposed pairs, ascending from the inner basal angle; style very short, obtuse or minutely capitate, the stigmas obscure or minute and alternate with the stamens. *Fruits* several per inflorescence, of 3 capsular mericarps, these divergent, separately attached to a swollen receptacle, flattened on both surfaces, obtuse or subacute and slightly swollen at the base, sharp and entire at the margins, dehiscing along an inconspicuous, median suture, the pericarp papyraceous or thin-coriaceous; seeds 2-8 per mericarp, the embryoniferous portion somewhat flattened, affixed by a conspicuous, membranous, basal wing.

A neotropical genus of nine species, one of which occurs in Panama.

1. PRISTIMERA NERVOSA (Miers) A. C. Smith, Brittonia **3:** 370. 1940.

Sicyomorpha nervosa Miers, Trans. Linn. Soc. London **28:** 412. 1872.

Liana or small tree, the branchlets elongate, subterete or distally subquadrangular. *Leaves* with the petiole 8-15 mm. long, the blade elliptic or broadly ovate-elliptic, obtuse or acute and decurrent at the base, obtusely acuminate at the apex, undulate or crenate at the margins, 7-20 cm. long and 3-9 cm. broad, papyraceous or chartaceous, the costa strongly elevated above, prominent beneath.

Inflorescences 2.5-7 cm. long, the distal nodes contracted at the base and appearing articulate, the bracts and bractlets conspicuous. *Flowers* 1.7-3.5 mm. in diam., the pedicel slender, less than 1 mm. long; sepals ovate-deltoid or suborbicular, erosulous or conspicuously dentate at the margins, 0.5-0.7 mm. long and 0.7-1.3 mm. broad, submembranous or papyraceous; petals suberect, elliptic-oblong, entire, 1.2-1.8 mm. long and 1-1.3 mm. broad, thin-carnose; disc pentagonous, about 0.1-0.3 mm. thick; stamens suberect, the filaments deltoid-liguliform, conspicuously broadened toward the base, 0.3-0.5 mm. long, the anthers about 0.2 mm. long and 0.3 mm. broad; ovary with 4-8 ovules per cell, the style about 0.1-0.2 mm. long, carnose. *Fruit* unknown.

Panama, Surinam, Venezuela, Peru, Bolivia and Brazil (Acre).

CANAL ZONE: along the Trinidad River, near sea level, *Pittier 4030!* (US).

12. HIPPOCRATEA L.

HIPPOCRATEA L., Sp. Pl. 1191. 1753, Gen. Pl. ed. 5, 498. 1754.

Lianas, the branches and branchlets usually opposite; milky latex present. *Leaves* opposite, petiolate, stipulate. *Inflorescences* axillary, usually many-flowered, cymose-paniculate, with supplementary branchlets in the dichotomies or in the axils of branchlets, pedunculate, the branchlets elongate. *Flowers* hermaphrodite, small or medium-sized, pedicellate, bracteolate; sepals 5, subequal; petals 5, subimbricate or valvate, transversely barbellate within; disc continuous, annular-pulvinate, conspicuous, cupuliform, carnose, minutely tomentellous-papillate without; stamens 3, suberect or spreading and reflexed, the filaments often connate to the upper portion of the disc, the anthers often slightly extrorsely nutant, transversely ellipsoid, dehiscing by apical, transversal, confluent clefts; pollen grains in tetrads; ovary completely immersed in the disc, deeply sulcate, 3-celled, the cells 6- to 8-ovulate, the ovules 2-seriate, ascending from the inner basal angle; style subulate, truncate, the stigmas inconspicuous. *Fruits* 1-3 per inflorescence, of 3 capsular mericarps, these divergent, suberect, separately attached to a swollen receptacle, flattened dorsoventrally, dehiscing along an inconspicuous, median suture, the pericarp papyraceous or thin-coriaceous; seeds 5 or 6 per mericarp, affixed by a conspicuous, basal wing.

A genus of three species, one in tropical America and two in tropical Africa.

1. HIPPOCRATEA VOLUBILIS L., Sp. Pl. 1191. 1753; Standley, Contr. Arnold Arb. **5:** 94. 1933; A. C. Smith, Brittonia **3:** 359, *fig. 1.* 1940; Johnston, Sargentia **8:** 188. 1949.—Fig. 1(G, H).

Hippocratea obcordata Lam., Tab. Encycl. Méth. **1:** 100, *tab. 28 (1)*. 1791; Hemsl., Biol. Centr.-Am. **1:** 193. 1880.
Hippocratea ovata Lam., loc. cit. 100, *tab. 28(2)*. 1791; Hemsl., loc. cit. 193. 1880; Woodson & Schery, Ann. Missouri Bot. Gard. **29:** 357. 1942.
Hippocratea discolor G. F. W. Meyer, Primit Fl. Essequeboensis 19. 1818; Seem., Bot. Voy. Herald 90. 1853.
Hippocratea serrulata Miers, Trans. Linn. Soc. London **28:** 344. 1872; Hemsl., loc. cit. 194. 1880.
Hippocratea versicolor Miers, loc. cit. 350. 1872; Hemsl., loc. cit. 194. 1880.

Liana up to 25 m. long, the young parts densely and minutely brown-tomentellous-papillate, the branches often stout, terete, subterete or distally quadrangular, inconspicuously lenticellate. *Leaves* with the petiole slender, canaliculate or narrowly winged distally, 4-10 mm. long; blade ovate to elliptic or oblong-elliptic, rounded or acute at the base, rounded or obtusely cuspidate or short-acuminate at the apex, subentire, crenate or serrate at the margins, 4-17 cm. long and 2-8 cm. wide, chartaceous or rarely thin-coriaceous, the costa slightly or sharply elevated above, prominent beneath. *Inflorescences* 3-15 cm. long, the axes densely and minutely brown-tomentellous-papillate. *Flowers* 4-8 mm. in diam., the pedicel slender, 1-3 mm. long, tomentellous-papillate, the bracteoles about 0.5 mm. long and caducous; sepals broadly ovate to deltoid, rounded, obtuse or obscurely apiculate at the apex, erose or irregularly ciliolate at the margins, 0.5-1.2 mm. long and 0.6-1.4 mm. broad, papyraceous, minutely tomentellous-papillate; petals oblong or elliptic-oblong, subacute at the apex, minutely ciliolate at the margins, 2.5-4 mm. long and 1.3-2.6 mm. broad, minutely tomentellous-papillate especially outside, transversely barbellate inside about 1 mm. below the apex; disc 0.8-1.7 mm. high, often subpentagonous and sometimes expanded at the base; filaments ligulate, broadly expanded and often contiguous at the base, membranous or submembranous, sometimes minutely puberulus; anthers about 0.3-0.5 mm. long and 0.5-0.7 mm. broad; ovary about 1 mm. in diam., the style 0.8-1.3 mm. long. *Mericarps* obovate-elliptic or narrowly elliptic, obtuse and slightly swollen at the base, rounded or emarginate at the apex, subacute and entire at the margins, 4-8 cm. long, 1.5-5 cm. broad and 2-4 mm. thick before dehiscence, the pericarp usually densely and finely flabellate-costate without, smooth within; seeds with the embryoniferous portion obliquely ellipsoid, 13-25 mm. long and 4-7 mm. broad, the wing obovate-oblong, slightly falcate, 2-4 cm. long and 1-1.5 cm. wide.

Southern Florida and central Mexico southward to northern Argentina.

BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1059!* (MO, US); id., Water Valley, *von Wedel 1685!* (MO, US), *1839!* (MO, US). CANAL ZONE: Chagres, Isthmus of Panama, *Fendler 53!* (MO, US, syntype of *H. serrulata*); Barro Colorado Island, *Aviles 992!* (F), *Killip 40031!* (US), *Shattuck 992!* (MO), *1041!* (F), *1109!* (F), *Wetmore & Abbe 87!* (F), *160!* (F), *Woodworth & Vestal 483!* (F), *583!* (F); drowned forest of Río Puente near junction with Río Chagres, alt. 66 m., *Dodge, Steyermark & Allen 16825!* (MO); around Culebra, alt. 200-300 m., *Pittier 3333!* (F, US). COLÓN: along Río Fató, in forests or thickets, alt. 10-100 m., *Pittier 3384!* (F, US). DARIEN: Patiño, on cliffs along the beach, *Pittier 5704!* (US); along Río Tuira below El Real and Piriaque Island, *Stern, Chambers, Dwyer, Ebinger 893!* (MO, US); Bay of Ardita, *Seemann 1102* (K, type of *H. versicolor*). PANAMA: Río Pita, 1-3 miles above confluence with Río Maestra, *Duke 4739!* (MO); San José Island, *Johnston 529, 605!* (MO, US), *739!* (MO, US), *1143*. PROVINCE UNKNOWN: *Duchassaing s. n., Hayes 595.*

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Volume LII No. 2

Annals of the Missouri Botanical Garden

May, 1965

PUBLISHED QUARTERLY BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN
AND WASHINGTON UNIVERSITY PRESS
ST. LOUIS, MISSOURI

Annals
of the
Missouri Botanical Garden

A quarterly journal containing scientific contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

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Information

THE ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Beginning with Volume 45, 1958:

Subscription Price .... $15.00 per volume
Single Numbers .... 4.00 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Beginning June 1, 1962 the Stechert-Hafner Service Agency, Inc., 31 East 10th St., New York 3, N. Y., became sole agent for the ANNALS OF THE MISSOURI BOTANICAL GARDEN. The Agency handles all subscriptions, all claims beginning with volume 50 (1963) and all requests for back issues. Out-of-print numbers will be reprinted as may be required.

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// Annals
of the
Missouri Botanical Garden

Vol. LII May, 1965 No. 2

MONOGRAPH OF ROSA IN NORTH AMERICA. V. SUBGENUS HESPERHODOS[1, 2]

By Walter H. Lewis

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The subgenus *Hesperhodos* Cockerell ex Rehder of the genus *Rosa* includes a small number of species endemic to southwestern North America. Only four species have been proposed, *R. minutifolia* Engelm., *R. mirifica* Greene, *R. stellata* Wooton, and *R. vernonii* Greene, and these species as well as a consideration of the infrageneric status of the group will be discussed in this study.

INFRAGENERIC STATUS

Based on *Rosa minutifolia*, Crèpin (1889a) erected the section *Minutifoliae* and defined it as having few, small, incised leaflets, bractless pedicels, pinnate and erect sepals, narrow stipules with dilated and divergent auricles, and few, basally inserted achenes. Crèpin recognized 14 other sections in the subgenus *Eurosa* (= subg. *Rosa*) and, although he made no suggestion regarding the relationship of the new section to these, his arrangement: *Pimpinellifoliae* DC., *Luteae* Crèp., *Sericeae* Crèp., *Minutifoliae* Crèp., suggests a sequence of what he believed to be allied sections. In his revised classification of *Rosa* based on anatomical data, *Parmentier* (1898) maintained Crepin's *Minutifoliae,* but proposed a derivation of the section from the *Cinnamomeae* as a minor branch.

In this century the section *Minutifoliae* has been incorporated into others as well as elevated to subgenus or genus. Baker (1905) and Schwertschlager (1910) included it with the *Spinosissimae* Thory (= *Pimpinellifoliae*). Even though members of these sections have several features in common (Engelmann, 1882; Baker, 1902), these are, according to Boulenger (1937), examples of parallel evolution in

[1] Other parts in this series include: I. *R. acicularis,* Brittonia **11:** 1-24. 1959; II. *R. foliolosa,* Southwest. Nat. **3:** 145-153. 1959. III. *R. setigera,* Southwest. Nat. **3:** 154-174. 1959; and IV. R. × *dulcissima,* Brittonia **14:** 65-71. 1962.

[2] This study was supported, in part, by grant no. G-21818 from the National Science Foundation.

Ann. Missouri Bot. Gard. **52**(2): 99-113. 1965.

The previous issue of the Annals of the Missouri Botanical Garden, Vol. **52,** No. 1, pp. 1-98, was published on March 31, 1965.

the genus rather than indications of close affinity. Baker (1905) also included typical species of the sections *Caninae, Luteae,* and *Cinnamomeae* in his concept of the *Pimpinellifoliae* which, I think, illustrates a poor understanding of sectional classification in *Rosa.* Herring (1925), however, concluded that *Minutifoliae* and *Pimpinellifoliae* are distinct but related sections separated respectively by the basal insertion of the achenes and the pinnate sepals in *Minutifoliae,* and by the basi-parietal insertion of the achenes and the entire sepals in *Pimpinellifoliae.*

Following an examination of the species in the field, Cockerell (1913) judged that a rank above that of section was required for the *Minutifoliae.* He gave no evidence, however, to support his proposal that the group should be recognized as either the genus or subgenus *Hesperhodos.* The first data in support of this view were presented by Hurst (1928) who concluded on the basis of a gametic chromosomal analysis that the section should be treated as a distinct genus. According to Hurst, *R. minutifolia* as well as *R. persica* Michx., *R. microphylla Roxb.* (= *R. roxburghii* Tratt.) and *R. bracteata* Wendl. do not correspond to any of the basic diploid septets in *Rosa* and must, therefore, be recognized as belonging to four different genera. Erlanson (1931) questioned this theory and she showed conclusively that there is no cytological basis for Hurst's septet analysis. Elsewhere, Hurst (1929) reported that he was unable to cross *Hesperhodos minutifolia* with *Rosa* which he thought substantiated his earlier conclusion, but long before, Cockerell (1913) noted a successful hybridization between *R. stellata* Wooton (a subspecies of *H. minutifolia* sensu Hurst) and an unnamed species of *Rosa* s. s.

Largely because of the unusually wide orifice of the hypanthium, Boulenger (1937) also recognized *Hesperhodos.* While this is a rare character in *Rosa,* it is typical of *R. roxburghii* which was assigned to *Platyrhodon* by Hurst (1928), but Boulenger retained the species in *Rosa.* He also emphasized the similar leaf morphology of *Hesperhodos* with that of *Alchemilla, Horkelia,* and *Potentilla,* striking similarities which might be considered examples of parallel development in the *Rosaceae.* To these can be added the similar leaf morphology of *Hesperhodos* and members of *Rosa* sect. *Pimpinellifoliae.* Without discussion, Rehder (1940, 1949) adopted Cockerell's (1913) subgeneric rank for *Hesperhodos.*

The data presented since Crépin to establish the infrageneric position of the *Minutifoliae* or *Hesperhodos* group are not convincing. It now remains to summarize the existing evidence, to present several new features, and from these to suggest the most applicable rank.

Gross Morphology.

In common with a majority of the species of *Rosa,* the taxon consists of woody perennials having alternate, pinnate leaves with adnate stipules and serrated leaflets, and perfect flowers of numerous stamens and pistils with the latter inserted at the bottom of well-developed hypanthia. Characteristics which suggest an isolated position for the taxon are the small, often incised leaflets, the thick, cupulate hypanthia each having a broad orifice, and the long, non-angular achenes. Generally, but not universally, the leaflets of *Rosa* species are larger and only serrated, the hypanthia are thinner-walled, contracted apically, and the achenes are ± angular.

Pollen Morphology.

Following a study of pollen from a limited number of *Rosa* species, Crépin (1889b) and Parmentier (1898) reported no difference in morphology and later Wodehouse (1935) and Erdtman *et al.* (1961) again noted that different species of *Rosa* are palynologically alike. None examined pollen of the species under review.

Acetolyzed grains of *R. minutifolia* and all subspecific taxa of *R. stellata* were examined and found to be subspheroidal (subprolate), 23.6-27.9 μ (E) × 20.1-24.6 μ (P), 3-colporoidate, with colpi long (ca. 18 μ), narrow, and slightly constricted equatorially with the delimiting exine somewhat thickened and irregular, ora about 2 μ high and delimited by a diffuse, irregularly outlined, thin (nexinous ?) area, apocolpium ca. 4 μ in diameter, sexine thin (less than 1 μ), O-L pattern, finely reticulated, and nexine about ⅔ thickness of sexine. Pollen of all taxa was indistinguishable and the description is by and large applicable to all species of *Rosa* with the exception of one characteristic, namely, the sculpturing of the sexine. For *R. minutifolia* and *R. stellata* the outer surface of the pollen is finely reticulated, whereas the sculpturing for all others examined (including species of the sections *Cinnamomeae, Synstylae, Caninae, Indicae, Pimpinellifoliae*) and as described for *R. rugosa* Thunb. (Wodehouse, 1935) and *R. acicularis* Lindl. (Erdtman *et al.*, 1961) is finely striated. Since this survey includes pollen of *R. pimpinellifolia* L. the results support Boulenger's (1937) opinion of parallelism between the sections *Pimpinellifoliae* and *Minutifoliae* rather than of close affinity.

Stem Anatomy.

After a survey of stem anatomy in roses Parmentier (1898) reported that members of the sections *Minutifoliae* and *Microphyllae* alone possess bast fibers. Moreover, he found that the pericycle of *R. minutifolia* consisted of short, ovate cells, whereas for all other *Rosa* examined these cells were elongate and fusiform. These data also suggest an isolated position for the taxon.

Chromosome numbers.

Hurst (1928) reported *R. minutifolia* with $n = 7$ and $2n = 14$, numbers confirmed by Erlanson (1932) who also found the same somatic numbers for *R. mirifica* Greene and *R. stellata* Wooton. To these are now added numbers for *R. stellata* subsp. *mirifica* collected 0.3 miles S. of High Rolls, Otero Co., New Mexico (*Lewis* 5527), having $2n = 14$ for five individuals and $2n = 16$ for one plant. Trisomics are rare in *Rosa*, but Erlanson (1929) also recorded this number for *R. pyrifera* Rydb. (= *R. woodsii* Lindl.) and *R. blanda glandulosa* Schuette (= *R. blanda* Ait.) from among plants with typical diploid numbers. These counts are in agreement with those for all other *Rosa* species studied which, with the exception of the few aneuploid individuals, are based on $x = 7$.

Do these data aid in evaluating the most satisfactory rank for the taxon? They show that it can be distinguished from most other *Rosa* by several well-marked gross morphological features unquestionably greater in number and in kind than are presently known for differentiating the species into sectional groupings. More-

over, observed differences in pollen and cells of the stem emphasize the need to recognize the group above that of section. But the chromosomes of this taxon are similar in number to those of *Rosa,* successful hybridization has been reported between one species of this taxon and a "true" rose, and many gross morphological and palynological characters are common to both and not common elsewhere in the family. On weighing these differences and similarities, I suggest a rank of subgenus for this taxon.

THE SPECIES

Gross Morphology.

In the subg. *Hesperhodos, R. minutifolia* is separable from the other species by having very small, 5- to 7-foliolate leaves, pilose floral branches with brown, pubescent thorns, and tomentose hypanthia with many, long prickles. Under the oldest name of *R. stellata,* the remaining taxa form a complex of closely allied populations characterized by stellate hairs or gland-tipped bristles on their floral branches. Greene (1910) described *R. vernonii* as distinct from *R. stellata,* but Rydberg (1918) later placed the species in synonymy under *R. stellata.* Greene also segregated those plants lacking stellate hairs as *R. mirifica,* a procedure followed by Rydberg (l. c.), but Cockerell (1914) reduced the species to a variety of *R. stellata* and this status was later accepted by Rehder (1927, 1940, 1949).

Greene (1910) separated *R. mirifica* from *R. stellata* by the following criteria:

	stellata	*mirifica*
(1) growing stems	stellate-tomentose by trichomes around short murications	without trichomes around the many, short, often gland-tipped prickles
(2) leaflets	small mostly 3, sometimes 4 or 5 pubescent pustulate-roughened above	twice size of *R. stellata* commonly 5 glabrous not pustulate or roughened above
(3) stipules	short, surpassed by large foliaceous auricles	long, their small auricles not notably foliaceous

In order to test the value of these, eight collections (each consisting of about 10 plants) were collected in New Mexico and analyzed.

Using only floral branch indumenta, three of the mass collections could be placed with *R. stellata* and three collections with *R. mirifica.* The remaining two collections consisted of plants combining some expressions supposedly confined to each species. As an illustration of the kind of stem indumentum typical of *R. stellata,* Fig. 1 shows a portion of the branch covered with short murications (glandlike excrescences) having stellate hairs and long, basally-pubescent, broad-based thorns usually paired below the stipules. Sometimes there are more than two thorns and occasionally they are internodal. Infrequently short, gland-tipped bristles with

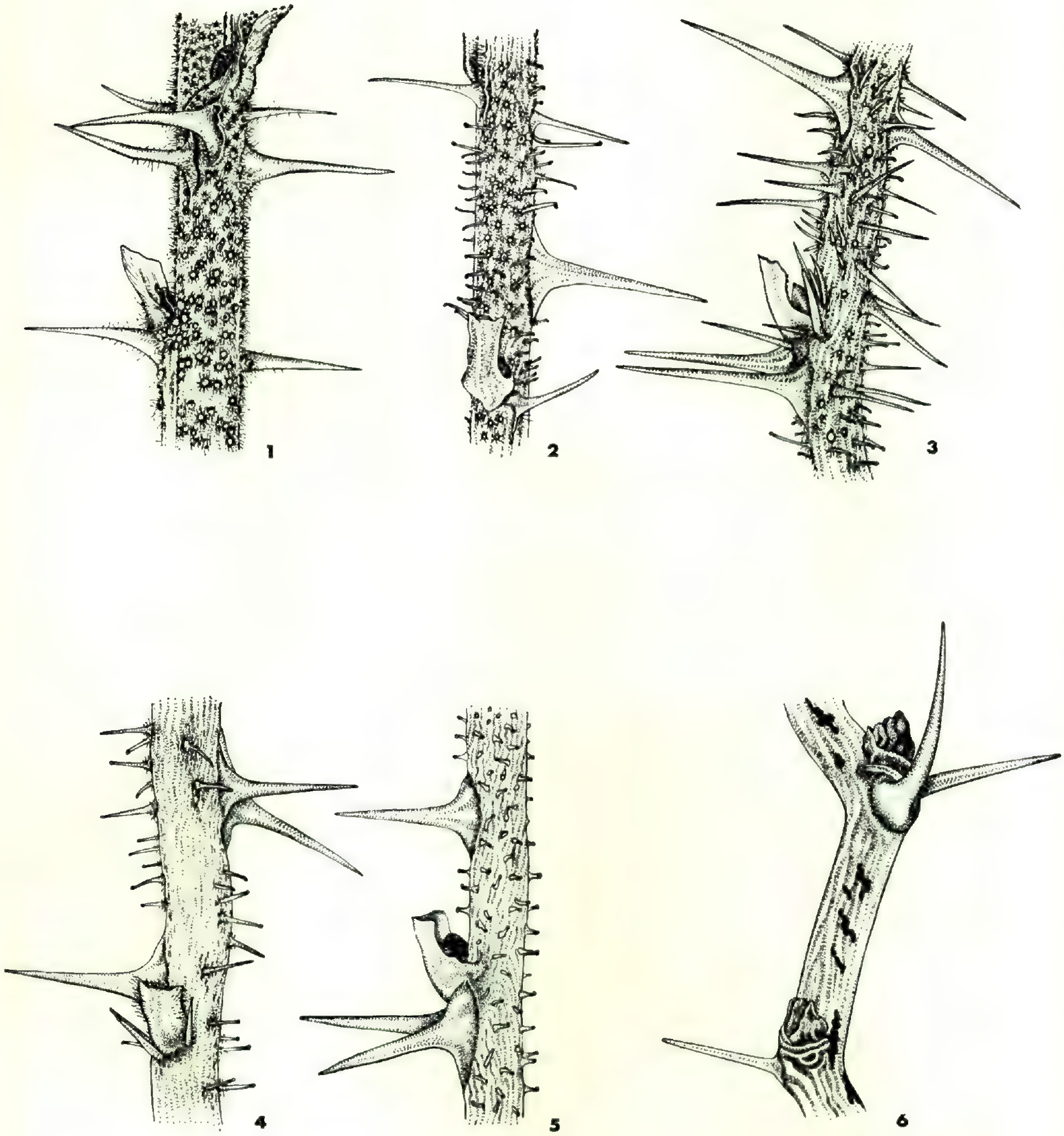


Fig. 1-6. Floral branches showing variations in indumentum for individuals of the *R. stellata* complex, 4 × Figs. 1-3. *R. stellata* Wooton subsp. *stellata* (*Lewis 5521, 5523, 5519,* respectively). Figs. 4-5. *R. stellata* subsp. *mirifica* (Greene) W. H. Lewis (Lewis 5529, 5527, respectively). Fig. 6. *R. stellata* subsp. *mirifica* var. *erlansoniae* W. H. Lewis (*Hinckley 18*).

Table 1. Expressions for five characters involving eight mass collections and two types of the *R. stellata* complex.

Character	Expression	Taxon and Collection				
		stellata (—)[a]				
		syntype	5521	5522	5523	5519[b]
Leaflet number	three	—	—	±	±	—
Leaflet size	< 10 mm. long & 6 mm. wide	—	+	+	+	—
Leaflet indumentum	pubescent	—	+	—	—	—
Leaflet texture	roughened	—	±	—	—	+
Stipule/auricle	stipule shorter than auricle or about equal	—	—	±	±	+
		mirifica (+)[a]				
		isolectype	5527	5532	5534	5529[b]
Leaflet number	five	±	±	—	±	—
Leaflet size	> 10 mm. long & 6 mm. wide	+	+	—	+	+
Leaflet indumentum	glabrous	+	±	+	—	—
Leaflet texture	smooth	±	+	+	±	+
Stipulate/auricle	stipule long (ca. 6 mm.), auricle short (ca. 3 mm.)	+	±	+	+	—

[a] Expressions typical of *R. stellata* (—) and those typical of *R. mirifica* (+) while ± represents both expressions on the same plant or for different plants of the same mass collection or for both.

[b] Atypical mass collections based on floral stem indumentum.

basal hairs are also found. That this characteristic indumentum is not universal for the species is obvious on comparing it with the indumentum from a plant of a second collection (Fig. 2). In this instance, the murications having stellate hairs are fewer, the bristles, either gland-tipped or lacking glands, are more numerous and vary in size, and they either possess basal hairs or they are glabrous. For plants of a third mass collection, the stem murications are even fewer and some possess stellate hairs while others do not; in addition, the frequency and variation of internodal bristles and prickles is much greater (Fig. 3).

Branches of typical individuals of *R. mirifica* lack pubescence and murications, but they are covered with many gland-tipped bristles and long nodal and internodal thorns (Fig. 5). This kind of indumentum may vary. Bristles and prickles differ in size, some are gland-tipped while others are not, usually they are glabrous, but rarely do they possess basal hairs (Fig. 4) similar to *R. stellata*. Even for this limited sample, a fairly complete range of kinds of indumenta exist from those having numerous murications with stellate hairs characteristic of *R. stellata* to those having very few gland-tipped bristles, no murications, and glabrous branches typical of *R. mirifica*.

The latter expressions represent dominant extremes in the populations and although the number of individuals varying from such characterizations are fewer, they do represent significant elements in the complex as a whole. The sample illustrates that some plants of both populations have varying amounts of pubescence on their floral branches and are not just glabrous or pubescent. The sample also shows that plants having many internodal gland-tipped bristles are found in both populations and are not confined to one or to the other. Unless a meaningful separation on the basis of floral branch indumentum is to be found, obviously the basis of discontinuity between the populations must be redefined and of necessity be considered in a more restricted form. One minor characteristic only appears to hold up, i. e., the presence of stellate-like hairs on short murications for *R. stellata* and the absence of these murications and hairs for *R. mirifica*. Yet for *R. stellata* (Fig. 3) these may be very few in number so even this criterion must be used with caution.

Using Greene's (1910) other diagnostic characteristics, what separation has been found possible for these eight mass collections? Considering first the syntype of *R. stellata* (*Wooton 126*, MO), I have shown in Table 1 that this individual matches precisely Greene's description. On the other hand, the isolectotype of *R. mirifica* (*Wooton 193*, MO) prominently differs from the type description by having commonly three rather than five leaflets per leaf and somewhat roughened leaflet surfaces even though these were described as smooth. Among the mass collections determined as *R. stellata* by their floral branch indumentum, all possess one or more expressions of leaf and stipule morphology supposedly typical of *R. mirifica*. Significantly, all "distinguishing" characters are involved but most commonly leaflet number and size. The same is true for those collections determined as *R. mirifica*: all include plants expressing some characteristic which should be confined to *R. stellata*, but notably leaflet number, size and indumentum. In summary of the data outlined in Table 1, one finds that for:

R. stellata, leaflet number—1/3 plants are *R. mirifica* in expression
leaflet size—all plants are *R. mirifica* in expression
leaflet indumentum—1/3 plants are *R. mirifica* in expression
leaflet texture—1/6 plants are *R. mirifica* in expression
stipule/auricle—1/3 plants are *R. mirifica* in expression

R. mirifica, leaflet number—1/3 plants are *R. stellata* in expression
leaflet size—2/3 plants are *R. stellata* in expression
leaflet indumentum—1/2 plants are *R. stellata* in expression
leaflet texture—1/6 plants are *R. stellata* in expression
stipule/auricle—1/6 plants are *R. stellata* in expression

The above shows that all five criteria are unreliable for separating the populations into two taxa. Clearly Greene's (1910) assumption of their value was premature.

Elimination of these characters leaves only the presence or absence of stellate-like hairs on the floral branches as the discontinuous characteristic by which the populations may be distinguished, although, as I have outlined above, even this

feature is somewhat variable. Transferring these results to a practical and meaningful classification requires, in my opinion, a subspecific (subspecies or variety) rather than a specific rank for populations named *R. stellata* and *R. mirifica.*

Distribution.

Species of the subg. *Hesperhodos* are endemic to two widely separated areas of North America (Fig. 7): *R. minutifolia* to western Baja California Norte, and the *R. stellata* complex to south-central New Mexico and far western Texas. In New Mexico, the latter is found at altitudes of 5,000 feet or higher on two north-south ranges—the San Andres range, including the Organ Mountains to the west, and the Sacramento range, including the Sierra Blanca Mountains, to the east. Between these ranges is the xeric Tularosa Valley supporting little vegetation and no roses under conditions perhaps best illustrated by the existence there of the White Sands National Monument. On the mountain slopes plants typical of *R. stellata* are found only on the San Andres range, whereas those typical of *R. mirifica* are confined to the Sacramento Mountains. Even so-called atypical plants are known only on mountain ranges inhabited by typical plants of each species.

In Texas, *R. stellata* s. s. is not known, but *R. mirifica* is found on an extension of the Sacramento range called the Guadalupe Mountains as well as further to the south. The greatest variability of the taxon is in this area and a distinct variety (Fig. 6), apparently confined to McKittrick Canyon, will be described.

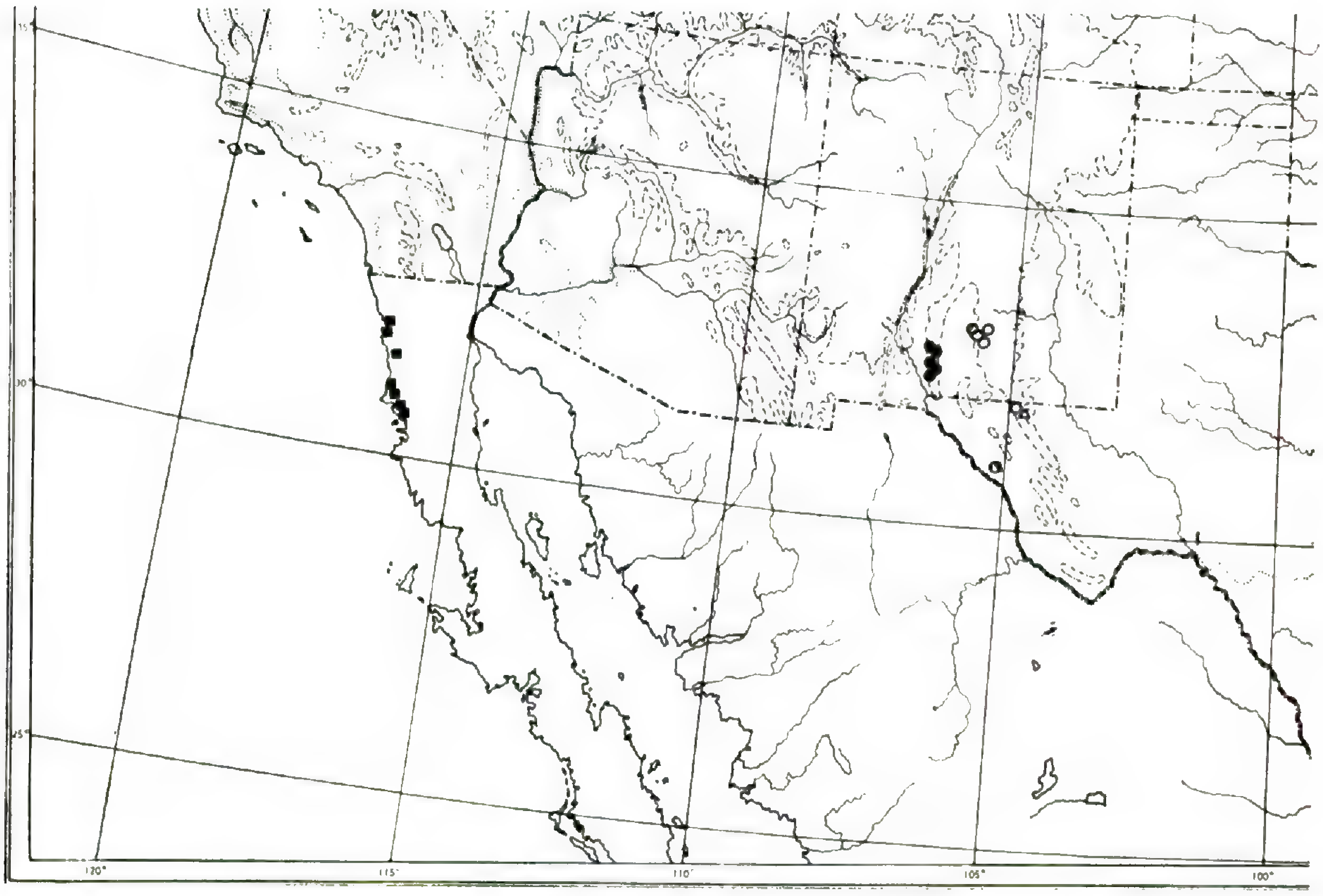


Fig. 7. Distribution of *R. minutifolia* Engelm. (■) and the *R. stellata* Wooton complex as subsp. *stellata* (●), subsp. *mirifica* (Greene) W. H. Lewis var. *mirifica* (○), and subsp. *mirifica* var. *erlansoniae* W. H. Lewis (△).

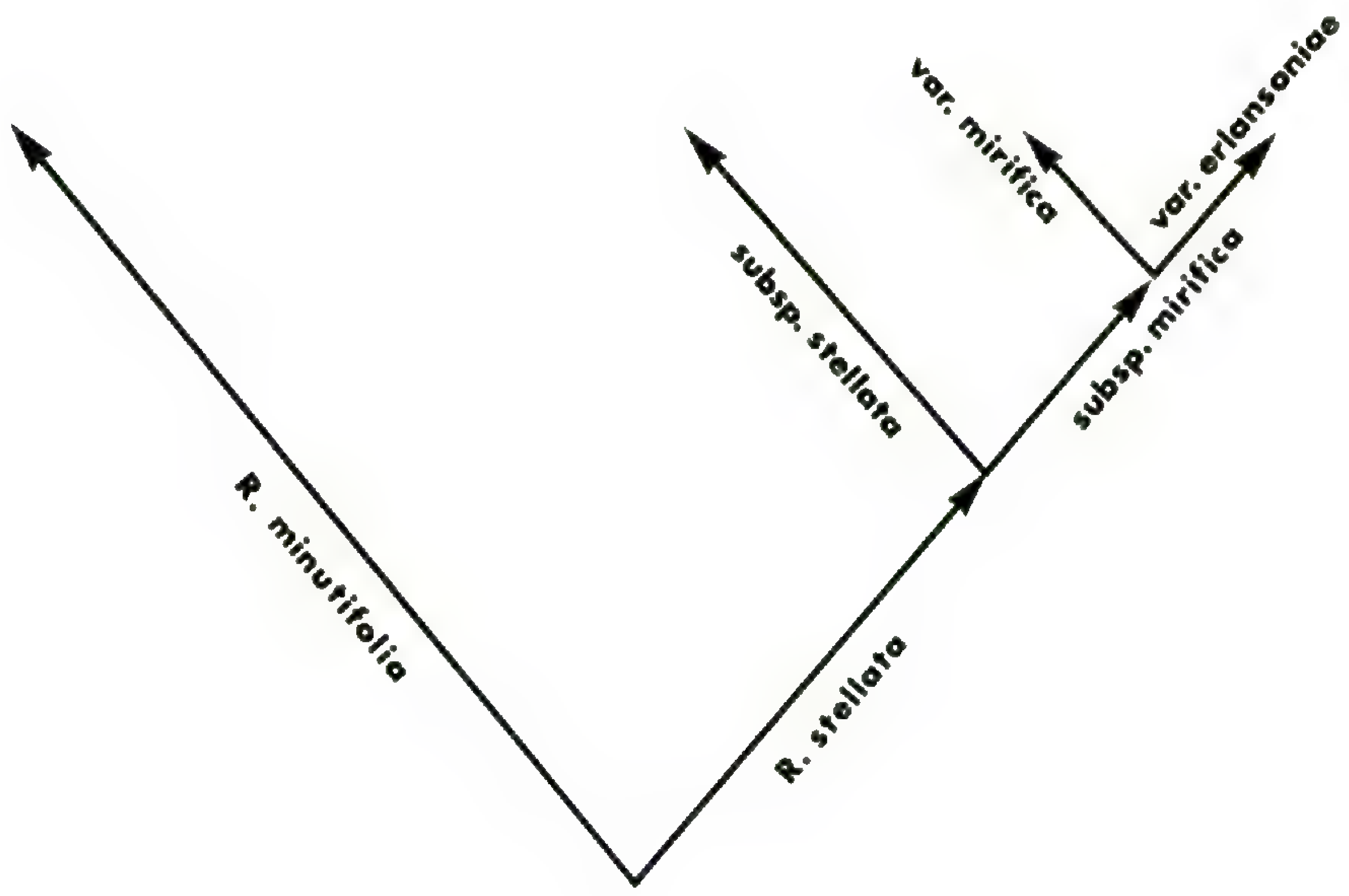
On the basis of gross morphological and supporting distributional data, the populations of the *R. stellata* complex are divisible into two subspecies as *R. stellata* subsp. *stellata* and *R. stellata* subsp. *mirifica.*

Phylogeny.

The existence in the San Andres and Sacramento Mountains of plants with some floral branch characteristics similar to one another, but not typical of the subsp. *stellata* and subsp. *mirifica,* respectively, suggests that the two subspecies are not effectively isolated and that a gene exchange is possible or has recently taken place. Yet the intervening and formidable desert makes such a possibility unlikely. Assuming that the present day populations were continuous in distribution under more favorable circumstances, the original population was probably more homogeneous and was not characterized by either of the forms known today. Thus the tomentose-woolly stellate-like hairs which now typify stems of one population and the concentrated gland-tipped bristles and glabrous stems of the other would be the specialized products of isolation. However, the atypical elements of each population today are so similar that they nearly bridge the gap between the two subspecies. This phenomenon could be explained if in fact the near-intermediate, less distinctive stem indumentum approached that of the original population which is still represented on both mountain ranges by plants possessing original indumental characteristics. Only occasionally would the necessary recombinants come together to produce an individual with the "ancient" now atypical phenotype for indumentum. Providing that this hypthesis is correct, I suspect that such individuals will become even fewer as the two separate populations evolve along distinct pathways. Ultimately, with the loss in both populations of somewhat similar indumental characteristics and possibly by the selection of others, the specialization may eventually be recognized taxonomically above that of subspecies.

This evolution is probably a micro-example of what has taken place in earlier times for the subgenus as a whole, i. e., the species were at one time more homogeneous and were continuous in distribution. Today there are only two remnants of this population. One survives only along the Pacific coast of Baja California Norte, and the other is found about 600 miles to the east on certain mountain ranges of New Mexico and Texas. The geologic history of the southwest is ideal for explaining such discontinuities and isolations, and it is quite conceivable that following major disruptions in that region during Cretaceous and Tertiary times a more widespread phylad split into several segments and survived (with migration?) only in two small, widely disjunct areas. The existence of species populations in Baja California from what are believed to be ancient stocks is not uncommon to the peninsula with the most closely allied species far to the east and unknown in adjacent areas of Mexico and California (e. g., *Hedyotis* subg. *Edrisia;* Lewis, 1962).

The phylogeny of the taxa is summarized by the following sketch.



How old the species are is unknown for there is no fossil evidence (Cockerell, 1913) contrary to the reference by Hurst (1929). The primitiveness of the subgenus has been widely suggested (Cockerell, 1913; Hurst, 1928) and certain unique characteristics not known elsewhere in *Rosa* or confined to species endemic to areas of southern Asia support this proposal.

Systematic Treatment

Collections of the subgenus *Hesperhodos* have been examined from ARIZ, GH, K, MEXU, MICH, MO, MONT, NEB, S, SMU, SRST and US. To the directors and curators of these herbaria I express my sincere thanks for the opportunity of studying material under their charge. My collections are deposited with MO and duplicates have been distributed to MICH or SMU.

Rosa subg. Hesperhodos Cockerell ex Rehder, Cult. Trees & Shrubs, ed. 2, 451. 1940. Type: *R. stellata* Wooton.

sect. *Minutifoliae* Crépin, J. Roy. Hort. Soc. **11**: 226. 1889. Type: *R. minutifolia* Engelm.
sect. *Spinosissimae* sensu Baker, J. Linn. Soc., Bot. **37**: 74. 1905, pro parte, non DC.
subg. or genus *Hesperhodos* Cockerell, Nature **90**: 571. 1913.
Hesperhodos Cockerell ex Hurst, Zeitschr. Indukt. Abst. Vererb. suppl. **2**: 902. 1928.

Shrubs with prickly stems 0.5 to 1.3 m. long; leaflets small, 3-7, incised-serrate; stipules adnate with divergent, often broad auricles; flowers solitary, peduncles without bracts; sepals erect after flowering, persistent, the outer pinnate with spreading appendages; hypanthia cupulate, thick-walled, bristly, with broad orifices; achenes few to ca. 15, oval, to 5 mm. long, borne at the base of hypanthia; styles free, included, persistent; pollen small, subprolate, 3-colporoidate, sexine finely reticulated; diploid species ($x = 7$).

Two species endemic to xeric regions of southwestern North America.

KEY TO THE TAXA

a. Leaves 5-7-foliolate; leaflets very small, to 7 mm. long & 4 mm. wide; young floral branches with brown, pubescent thorns; hypanthia tomentose, densely covered with long, fine prickles; Baja California Norte. .... 1. *minutifolia*

b. Petals pink. .... 1a. f. *minutifolia*

bb. Petals white. .... 1b. f. *albiflora*

aa. Leaves 3-5-foliolate; leaflets usually larger, 7-20 mm. long & 4-17 mm. wide; young floral branches with white to yellow, occasionally puberulent thorns; hypanthia glabrous or puberulent, with scattered, short bristles; New Mexico & Texas. .... 2. *stellata*

b. Floral branches tomentose-woolly with long stellate hairs originating from many, short murications or obsolete gland-tipped bristles; internodal prickles few; infrequently branches pubescent with short hairs originating from internodal prickles and with fewer murications; San Andres Mts., New Mexico. .... 2a. subsp. *stellata*

bb. Floral branches glabrous with many internodal gland-tipped bristles and prickles and no murications, less commonly pubescent with basal hairs on internodal prickles; Sacramento Mts., New Mexico and in Texas. .... 2b. subsp. *mirifica*

c. Floral branches $\pm$ straight, densely covered with internodal bristles. .... 2bα. var. *mirifica*

cc. Floral branches angled at nodes, devoid of internodal bristles or rarely with few. .... 2bβ. var. *erlansoniae*

1. R. MINUTIFOLIA Engelm. in Parry, Bull. Torr. Bot. Club **9:** 97. 1882.

Shrub with numerous usually decumbent stems to 1.5 m. long; floral branches pubescent, densely armed with scattered, slender, long, broad-based thorns and with smaller prickles which when young are pubescent at the base and reddish-white, and with age, glabrate and gray-brown; leaves 5-7 foliolate; leaflets oval or suborbicular, 2-7 mm. long and 1-4 mm. wide, pubescent above and below, eglandular, margin incised, single or biserrate, often gland-tipped; petioles pubescent, occassionally glandular-hispid; stipules adnate, 5 mm. long or less, pubescent, glandular-dentate, auricles short, spreading; flowers solitary and terminal on short floral branches; peduncles short, to 5 mm. long, tomentose, bristly; sepals ovate, caudate, often with foliaceous gland-tipped lobes, broad-based, 6-10 mm. long, tomentose within, pubescent and usually bristly without, in fruit persistent and erect; petals suborbicular, deep rose to white (in f. *albiflora*), 10-15 mm. long; at maturity hypanthia globose, tomentose, densely covered with long, pubescent bristles; anthesis usually January-April; chromosome number $2n = 14$.

1a. R. MINUTIFOLIA Engelm. f. MINUTIFOLIA.

Hesperhodos minutifolia (Engelm.) Hurst, Zeitschr. Indukt. Abst. Vererb. Suppl. **2:** 902. 1928.

Type: MEXICO, Baja California Norte, All Saints' Bay, near Ensenada, *Parry and Jones s. n.*, 11 April 1882 (holotype, MO).

MEXICO: Baja California Norte, 9.8 miles N. of Calonia Guerrero, *Straw & Ownbey 526* (MEXU); [near] El Rosario, *Brandegee s. n.*, 20 May 1889 (GH), *Bravo s. n.*, 15 Nov. of *R. mirifica.*

1956 (MEXU); Ensenada, *Anthony 189* (GH, K, MEXU, MO, US), *Jones 3697* (MO, US), *Orcut s. n.*, 31 Jan. 1889 (MO); 50 miles S. of Ensenada, *Dressler 482* (GH, MO); 8 miles N. of Hamilton Ranch, *Shreve 6427* (ARIZ, MICH); Rancho Piedra Roja, Santo Domingo, *Galligas (?) s. n.*, 23 Febr. 1925 (MEXU, US); 7 miles N. of Rio Santo Domingo, *Ferris 8525* (MICH, US); San Quentin [Bay], *Palmer 619* (GH, K, MICH, S, US); near San Quentin, about 110 miles S. of border, *Nelson & Goodman 7103* (US); N. of San Quentin, San Antonio Cañon, *McKeever 29* (US); San Telmo, *Orcutt s. n.*, 18 Apr. 1886 (MO); 21 miles S. of Santo Tomás, *Wiggins 4272* (GH, MICH, SMU, US); Todos Santos Bay, *Orcutt s. n.*, 12 Apr. 1882 (MICH, MO), *Parry & Co. s. n.*, Apr. 1882 (GH), *Pringle 14504* (K, MO, US), *Pringle s. n.*, 12 Apr. 1882 (GH).

1b. R. MINUTIFOLIA Engelm. f. **ALBIFLORA** W. H. Lewis, f. nov.
Petala alba. Petals white.

Type: MEXICO, Baja California Norte, Todos Santos Bay, near Ensenada, *Erlanson, Emerson, and Beadle s. n.*, 1 April 1931 (holotype, MO; isotype, GH). The type collection is named *R. minutifolia* Engelm. var. *alba*, n. var., but to my knowledge the variety remains unpublished.

The white petaled form is said by Cockerell (1941) to be "not uncommon" and to form large patches around Ensenada and southward. Cockerell refers this variant to a listing by Gravereaux (1902) as "*R. minutifolia* f. *alba*," yet Gravereaux was listing not *R. minutifolia*, but rather a variety and form *R. multiflora* Thunb., viz., on page 155, section 1. *Syntylae, Rosa multiflora* ses variétés et ses hybrides, followed on page 156 with var. *minutifolia alba*. This suggests that Cockerell failed to read the previous page and so to properly associate the variants with *R. multiflora*, an opinion strengthened by the fact that Gravereaux had already listed the section *Minutifoliae* and *R. minutifolia* on page 49.

2. R. STELLATA Wooton, Bull. Torr. Bot. Club **25**: 152. 1898.

Shrub with numerous, upright or rarely trailing stems, 0.4-1.5 m. long; floral branches ± straight or infrequently angled (in var. *erlansoniae*), armed with long, white to yellow, broad-based, glabrous or puberulent basally, infrastipular and often internodal thorns, and covered with stellate hairs on mucronate axes (in subsp. *stellata*), or lacking hairs or with few, but possessing many small bristles and prickles commonly gland-tipped (in subsp. *mirifica*), or these few or absent (in var. *erlansoniae*); leaves 3-5 foliolate; leaflets cuneate-obovate, rounded or truncate at apex, 7-20 mm. long and 4-17 mm. wide, glabrous to pubescent, eglandular, with 5-12 serrations per leaflet, commonly all above the middle, obtuse or rounded, singly or biserrated, often gland-tipped; petioles glabrous or pubescent, but often glabrate, sometimes with few bristles; stipules adnate one-half or more, 5-10 mm. long, with auricles spreading, entire or glandular-dentate, glabrous or pubescent; flowers solitary, terminal; peduncles short, 10 mm. long or less, glabrous, eglandular or sparingly glandular-hispid; sepals ovate-lanceolate, broad-based, 12-20 mm. long, 2-3 lobed or occasionally more, entire or serrated, often glandular margined, tomentose within, usually bristly and puberulent or pubescent without, eglandular or glandular-hispid, in fruit persistent and erect; petals obovate, 22-30 mm. long and 20-25

mm. wide; at maturity hypanthia irregularly spheroidal, 12-20 mm. in diameter, glabrous or occasionally puberulent, with scattered bristles often gland-tipped; anthesis April-September; chromosome number $2n = 14(16)$.

2a. R. STELLATA Wooton subsp. STELLATA.

Hesperhodos minutifolia Engelm. subsp. *stellata* (Wooton) Hurst, Zeitschr. Indukt. Abst. Vererb. Suppl. **2:** 902. 1928.
H. stellatus (Wooton) Boulenger, Bull. Jard. Bot. État Brux. **14:** 234. 1937.

Lectotype: NEW MEXICO, Dona Ana Co., Organ Mountains, near the Cueva, *Wooton s. n.*, 30 April 1893 (US), on a dry, rocky hillside at an altitude of about 5,000 feet. Syntype: same locality, *Wooton 126*, 10 July 1897 (MO) (isosyntypes, GH, K).

NEW MEXICO, Dona Ana Co.: Organ Mountains, *Wooton s. n.*, 29 April 1899 (US), 6 May 1900 (MO, MONT), 26 May 1905 (ARIZ, MICH, US), *Wooton & Standley s. n.*, 10 July 1897 (US), 28 Sept. 1902 (US), 23 Sept. 1906 (US); San Andres Mountains, Ash Canyon, *Hershey s. n.*, 8 May 1936 (NEB), *Parker 2475, 2475a* (ARIZ), Ash Spring, *Wooton s. n.*, 23 Sept. 1912 (US), 24 May 1913 (US), Ropes Springs, *Lewis 5519*, St. Nicholas Canyon, *Lewis 5521;* New Mexico State University (cultivated, originally Organ Mountains), *Lewis 5522, 5523.*

Less variable than the following subspecies, the subsp. *stellata* nevertheless may occasionally have many internodal bristles rather than few or none, and stellate hairs from muricate axes may be rare rather than common (e.g., *Lewis 5519*).

2bα. R. STELLATA Wooton subsp. **MIRIFICA** (Greene) W. H. Lewis, stat. nov., var. MIRIFICA.

R. mirifica Greene, Leafl. Bot. Obs. **2:** 62. 1910.
R. vernonii Greene, Leafl. Bot. Obs. **2:** 63. 1910.
R. stellata Wooton var. *mirifica* (Greene) Cockerell, Gard. Chron., ser. 3, **55:** 50. 1914.
Hesperhodos minutifolia Engelm. subsp. *mirifica* (Greene) Hurst, Zeitschr. Indukt. Abst. Vererb. Suppl. **2:** 903. 1928.
H. mirificus (Greene) Boulenger, Bull. Jard. Bot. État Brux. **14:** 236. 1937.

Lectotype: NEW MEXICO, Otero Co. (as Lincoln Co.), White Mountains, 2 miles west of the Mescalero Agency, *Wooton 193*, 22 July 1897 (US), at an altitude of about 6,000 feet (isolectotype, MO). Syntype: NEW MEXICO, Otero Co., Sacramento Mountains, Fresnal, *Wooton s. n.*, August 1897 (US).

It was on the basis of the lectotype that Greene (1910) distinguished *R. mirifica* from *R. stellata*. Not all specimens distributed under the lectotype's collector and number (*Wooton 193*), however, are typical of the subsp. *mirifica*, for one, having a different locality (near Blozer's Hill, White Mountains, ARIZ) has pubescent bristles on the floral branches. Other individuals with pubescent bristles are indicated by an asterisk under specimens examined.

NEW MEXICO. Otero Co.: Alamo National Forest, head of Río Fresnal, *Barlow s. n.*, 12 Aug. 1911 (MO); near Cloudcroft, *Slater s. n.*, Aug. 1915 (US); 5.3 miles W. of Cloudcroft, *Lewis 5529**; 0.3 miles S. of High Rolls, *Lewis 5527;* 2 miles S. of High Rolls, *Dice s. n.*, 19 July 1927 (MICH)*; 2.5 miles W. of Mescalero, *Lewis 5534;* 1.5 miles below Mountain Park, *Hinckley 6512* (ARIZ); Fresnal, *Wooton s. n.*, Aug. 1897 (US), 21 July 1899 (MONT, US); Fresnal Canyon, nr. Mountain Park, *Rehder 390* (GH, K)*, *334* (GH)*; along Tularosa Creek, *Wooton s. n.*, 18 Aug. 1899 (US). TEXAS. Culberson Co.: Guadalupe Mountains, West Dog Canyon, *Warnock 12076* (SMU, SRST), Guadalupe Mountains, *Bailey 421* (US, holotype of *R. vernonii* Greene)*. Hudspeth Co.: Eagle Mountains, ca. 35 miles S. E. of Sierra Blanca, *Waterfall 6719* (GH, MO, SMU, SRST).

2bβ. R. STELLATA Wooton subsp. MIRIFICA (Greene) W. H. Lewis var. **ERLANSONIAE** W. H. Lewis, var. nov.

Hesperhodos vernoni sensu Boulenger, Bull. Jard. Bot. État Brux. **14:** 237. 1937, non *Rosa vernonii* Greene (1910).

A varietate typica ramulis floriferis nodis angulatis, palliole viridibus sine setis aculeisque internodialibus, interdum sparsum setosis aculeatisque et glabris differt.

Differs from the typical variety by having floral branches angled at nodes, pale green, devoid of internodal bristles and prickles or sometimes sparsely bristly and prickly, and glabrous.

Type: TEXAS, Culberson Co., Guadalupe Mountains, North McKittrick Canyon, *Moore and Steyermark 3540*, rocky stream bed, altitude 1,800 m. (holotype, MICH, Fig. 21 in Boulenger [1937]; isotypes, GH, MO).

TEXAS. Culberson Co.: Guadalupe Mountains, North McKittrick Canyon, *Correll 13950* (SMU), *Hinckley [& Hinckley] 18* (MO, SMU, SRST, US), *McVaugh 7412* (MICH, SMU); Guadalupe Mountains, between North and Main McKittrick Canyons, *McVaugh 7407* (MICH, SMU).

Boulenger (1937) recognized *R. vernonii* as distinct from *R. stellata* s. s. based not on the type of the former species which he did not examine, but rather on material of *Moore & Steyermark 3540.* Both collections originated in the Guadalupe Mountains of Texas and very probably this misled Boulenger into assuming their similarity. Actually, *R. vernonii* is a pubescent form of *R. stellata* subsp. *mirifica* var. *mirifica* (*Hesperhodos mirificus* Boulenger), whereas *Moore & Steyermark 3540* represents the newly described var. *erlansoniae,* named for Dr. Eileen W. Erlanson MacFarlane who pioneered the revision of the North American species of *Rosa.*

Summary.

Populations of *Rosa* subg. *Hesperhodos* are separable by geographical and morphological characteristics into two species, *R. minutifolia* and *R. stellata.* The former is relatively homogeneous, while the latter consists of a complex population divided geographically and morphologically into two groups, the subsp. *stellata* and *mirifica* including the rare var. *erlansoniae.*

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A REVISION OF THE GENUS WRIGHTIA (APOCYNACEAE)

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INTRODUCTION

The present study is intended to clarify the systematics of the apocynaceous genus *Wrightia*. Since its establishment by R. Brown (Mem. Wern. Soc. **1:** 73. 1811), extensive collections and many new species recorded in various regional floras have increased our knowledge of the genus; however no comprehensive study, except a brief synopsis by Pichon (Not. Syst. **14:** 77. 1951), has been made subsequent to the publication of De Candolle's Prodromus (A. De Candolle in DC., Prodr. **8:** 404. 1844).

The lack of understanding of the variability of species within the genus on the basis of a general treatment has created much confusion in specific delimitation. Furthermore, *Wrightia* has never been well circumscribed from its closely related neighbor *Pleioceras*. In spite of Pichon's partial revision, which was based upon the limited number of specimens deposited at the herbarium of the Muséum National d'Histoire Naturelle at Paris, little has been known concerning the specific delimitation and the major subdivision within the genus.

The preparation of an up-to-date account of *Wrightia* has also become desirable for a better understanding, since much new material has been collected recently in Africa, China, New Guinea and Australia; this has helped to distinguish more clearly certain species within the genus. Herbarium material constitutes the principal basis for this study and nearly all herbarium specimens and types of *Wrightia* available from 30 major herbaria throughout the world have been examined, thanks to the respective curators for their generous loans of material.

HISTORY

Wrightia was first proposed as a genus by Brown in honor of Dr. William Wright, a Scotch physician and botanist who had spent 18 years on the island of Jamaica. The genus at that time included 4 species, of which 2 (*W. antidysenterica* and *W. zeylanica*) had previously been included within *Nerium* by Linnaeus. In the same paper Brown also created a monotypic genus, *Balfouria,* which was found later to be congeneric with *Wrightia*.

Between 1809 and 1844, in spite of the establishment of *Wrightia* with its clearly diagnostic characters based on the structure of the seed and embryo, several species still were described from flowering specimens under the genera *Nerium, Strophanthus, Cameraria, Chonemorpha, Anasser* and *Hunteria*. At the time many new species were proposed by various authors, but most of them proved to be redescriptions of species previously named.

The first extensive and critical review of *Wrightia* was made by A. de Candolle (in DC Prodr. **8:** 404. 1844). He recognized only 14 species at that time and

Ann. Missouri Bot. Gard. **52**(2): 114-175. 1965.

placed them in 2 sections: *Bammatophyton* which, according to the present International Code, must now be referred to as § *Wrightia* since it includes the type specimen of the genus, *W. pubescens, and* § *Wallida.* The section *Bammatophyton* was characterized by the corolla tube as long as, or twice or rarely 3 times, the length of the calyx whereas § *Wallida* included species with a corolla tube about 6 times longer than the calyx. Actually, A. de Candolle seemed to suspect *Wallida* as a distinct genus by this statement: "Verisimiliter genus distinctum?" and this suggestion was effected by Pichon later on. For this section *Bammatophyton,* A. de Candolle recorded 12 species, among which 5 (*W. calycina, W. ovata, W. javanica, W. wallichii* and *W. laciniata*) were described as new. These species as well as 2 others previously described (*W. rothii* and *W. mollissima*) are not recognized as distinct in this study. His section *wallida* included 2 of Brown's species (*W. antidysenterica* and *W. zeylanica*) which are conspecific.

Bentham and Hooker (Gen. Plant. **2:** 712. 1876) published a synopsis of the genus, recognizing 12 species from tropical Africa, tropical Asia and Australia. They gave a short description of 2 new species, *W. religiosa* and *W. cunninghamii,* the latter with the corolla lobes dextrorsely contorted (never found in species of *Wrightia*), apparently an asclepiad.

In his treatment of the *Apocynaceae,* K. Schumann (in Engler and Prantl, Nat. Pflanzenfam. **4**(2):183. 1895) divided the then known species into 3 sections. He accepted A. de Candolle's two sections and created a third, *Gymnowrightia* which was characterized by the absence of a corona.

Until 1951, no general acount of the genus had been made on a world-wide basis. Only treatments of *Wrightia* for restricted floras and various scattered contributions had been recorded, such as Hooker's (Fl. Brit. Ind. **3:** 653. 1882.) contribution on species of India, Pitard's (Lecomte and Humbert, Fl. Gen. Indo-Chine **3:** 1182. 1933) treatment of the Indochinese species, Kerr's (in Craib, Fl. Siam. Enum. **2:** 456. 1939) study on species of Thailand, Chiovenda (Fl. Somola **2:** 290. 1932) and Stapf's (Kew Bull. **1907:** 51. 1907) works on the Somali and East African species respectively. These workers have greatly contributed to our knowledge of *Wrightia* and their studies are marked by a steady progress in circumscribing the genus.

In 1939, Y. Tsiang (Sunyatsenia **4:** 42. 1939) reviewed the Chinese species of *Wrightia* in the course of his study of Apocynales. Tsiang is a competent authority on the family and his work provides the first comprehensive study of *Wrightia* in China and adjacent lands. For the classification of the species he adopted K. Schumann's sections and offered a synoptic subdivision of *Bammatophyton* (= § *Wrightia*), the largest. He selected the corona scales as the most important character for distinguishing the different series. However, the diagnostic characters proposed in his classification for the separation of the series are not workable on a world-wide basis.

In 1951, with material available at the Muséum National d'Histoire Naturelle at Paris, Pichon (Not. Syst. **14:** 77. 1951) attempted to give a general account of the genus. He raised § *Wallida* to a genus with only 1 species and further split

Wrightia into 2 genera, *Wrightia* and *Scleranthera*, the latter including 2 species which I have found to be conspecific. His concept of raising the sections to the rank of genus appears to be undesirable since it creates, in place of a single well defined genus, a number of much less sharply defined smaller genera, 2 of them each with only 1 species. In his treatment, on the one hand, he reduced *W. laevis* to a variety of *W. tinctoria* and put *W. lanceolata* in synonymy under *W. tomentosa;* while on the other hand, he placed under the same specific name several apparently valid species such as *W. pubescens, W. flavido-rosea, W. puberula, W. sikkimensis* (= *W. schlechteri* and *W. stellata*) and *W. annamensis.* The last species, with the more or less included anthers and the monochasial inflorescences, is definitely distinct from *W. pubescens.* Apparently he was handicapped by the limited number of specimens available for his study, and thus produced some confusion by his work.

GENERIC RELATIONSHIPS

In spite of the many investigations which have been concerned with the *Apocynaceae*, the systematic position of *Wrightia* is still very puzzling. Alphonse de Candolle, in the *Prodromus*, recognized 7 tribes of *Apocynaceae*, and *Wrightia*, with its bicarpellary ovary and basally comose seed, was included within the *Wrightieae* between the *Parsonsieae* and the *Alstonieae* (characterized by apically comose and uniformly comose seed, respectively). Bentham and Hooker, in their *Genera Plantarum*, referred *Wrightia* to the subtribe *Parsonsiineae* of their tribe *Echitideae*. This subtribe was defined as having the corolla subrotate or salver-form and the anthers more or less exserted. However, the genus is rather closely related as well to their subtribe *Neriineae*, characterized by the presence of a coralline corona and included anthers provided with a long acumen. K. Schumann, in his treatment of *Apocynaceae* for the *Pflanzenfamilien*, raised the tribe *Echitideae* to the rank of subfamily, *Echitoideae*, and followed Bentham and Hooker in referring *Wrightia* to the *Parsonsieae* with the anthers exserted beyond the corolla tube, in contrast with the *Echitideae* characterized by the anthers inserted within the corolla tube. However, *Wrightia* as well as other genera of his *Parsonsieae*, such as *Prestonia* and *Malouetia*, embrace many species with included stamens.

In his treatise on the *Echitoideae*, *Pichon* (Mém. Mus. Natio. Hist. Nat., nouv. sér., sér. B, Bot. **1:** 1-174. 1950) proposed a new classification of the subfamily based upon the structure of the "retinaculum," an elaboration of the anther connective on the ventral side immediately below the sporangia. He therefore placed *Wrightia* in his *Nerieae*, which he defined as having a brush-like "retinaculum." On the basis of the seed structure with basal coma and convolute cotyledons, he put *Wrightia* close to *Kibatalia* and *Funtumia*, which Woodson (Philipp. Jour. Sci. **60:** 205. 1936) relates to *Forsteronia, Tintinnabularia, Beaumontia* and *Malouetia* on the basis of the presence of foliar foveae, differing in this respect from *Wrightia* which is destitute of these structures. Pichon even recognized the unnatural relationship of his *Wrightiineae* and *Kibataliineae* by this statement: "L'aigrette est basilaire et les cotylédons [of Wrightiineae] ne sont pas plans, tout comme chez les Kibataliineae. Mais là se borne le rapprochement, et il parait y avoir convergence plutôt que parenté réelle."

His system of classification of *Echitoideae* is not followed in this study since the so-called "retinaculum" has not proved of sufficient constancy and cannot be observed successfully in dried specimens.

I believe that *Wrightia* is most plausibly referred to the subtribe *Neriineae* in the traditional and narrower sense on the basis of the presence of a corona and the lack of nectaries. This subtribe includes, on the one hand, the genera *Nerium* and *Strophanthus*, which differ from *Wrightia* in the dextrorsely contorted corolla lobes, the apically comose seeds and the flat cotyledons and, on the other hand, *Pleioceras* and *Wrightia*. The most closely related genus to *Wrightia* appears to be *Pleioceras*, which shares with *Wrightia* these common characters: the sinistrorsely contorted corolla lobes, the presence of a well-developed corona, the basally comose seeds and the convolute cotyledons. Subsequently, in the past, *Pleioceras* has been often confused with *Wrightia* from which most taxonomists, following Stapf (in Thiselton-Dyer, Fl. Trop. Afr. **4**(1): 165. 1904), distinguished the former only on the basis of the pubescent body of the seed. Unfortunately, Stapf construed the frequent pubescence of the entire seed coat of *Pleioceras* as a decisive generic criterion, while I have found it to be fallible. On the other hand, Pichon stated that the body of the seed in *Pleioceras* is glabrous and the apparent pubescence is due to the reflexed coma appressed against the body of the seed. A careful examination of specimens available to my study indicates that the body of the seed in *Pleioceras* may be either glabrous, as in *P. gilletii*, or definitely pubescent, as in *P. zenkeri*. Actually, *Wrightia* and *Pleioceras* are quite distinct in other respects and sharply distinguished from each other. Their differentiating features may be summarized in the following tabulation:

Wrightia	*Pleioceras*
Inflorescence a dichasial or monochasial cyme.	Inflorescence a thyrse (save when depauperate).
Orifice of the corolla tube glabrous (except in *W. tinctoria* ssp. *rothii*).	Orifice of the corolla tube pubescent.
Alternating supplementary corona segments (when present) simple and never exceeding the antepetalous segments.	Alternating supplementary corona segments compound at the tips and at least twice as long as the antepetalous segments.
Staminal filaments not decurrent below the insertion within the corolla tube.	Staminal filaments decurrent below the insertion within the corolla tube.
Anthers sagittate-lanceolate.	Anthers sagittate-deltoid.
Body of the seed glabrous.	Body of the seed glabrous or pubescent.

MORPHOLOGY

Habit—Species of *Wrightia*, except *W. sikkimensis* of Assam which Fischer (Kew Bull. **1940**: 38. 1940) has described as a climber, are shrubs or small trees up to 20 m. in height. However the tallest species of the genus, *W. pubescens* and *W. laevis*, sometimes reach a height of 40 m. In the aboreal species the bole is rounded, columnar, without buttresses, and may attain, according to Whitford (The forests of the Philippines. Manila. 1911), a diameter of 6 dm. There are few available records about the texture, thickness and color of the bark. Twigs are slender and divaricate; however, in *W. demartiniana* they are outstanding within

the genus in being relatively short and crooked, a condition apparently due to the environment. This species is confined to the wooded steppe of Somalia, Ethiopia and Kenya.

Species of *Wrightia* may be deciduous, as in *W. tomentosa, W. tinctoria* and *W. demartiniana*, or evergreen, as in the remaining species. In deciduous species flowers appear together with young leaves. All the plants are lactescent and the latex is milky, however it may be yellow in *W. tomentosa*, which is used as a dye in India.

Leaves:—The leaves of *Wrightia* are simple and decussate; the leaf margins are entire throughout the genus. Leaves are variable in size and shape, but they provide fairly reliable characteristics for the distinction of many species. In size they range from 2 cm. long and 0.5 cm. wide in *W. demartiniana* to 24 cm. long and 9 cm. wide in some specimens of *W. tinctoria*. Leaf shape varies from linear-ovate, narrowly ovate to elliptic, broadly elliptic or obovate. *Wrightia angustifolia, W. natalensis, W. demartiniana* and *W. saligna* possess relatively narrow leaves, those of the latter linear-falcate with inconspicuous nerves. The apex of the leaf may be acute to acuminate or caudate-acuminate; the base is acute or occasionally obtuse.

Leaf venation is pinnate, the secondary veins oblique, more or less arcuate and united near the margins of the blade. The number of the secondary veins sometimes aids in the assignment of specimens to species within § *Wrightia*. In this respect leaves of *W. laevis* are outstanding with usually 6-9 pairs of secondary veins. The texture is mostly membranaceous, but in *W. antidysenterica, W. tinctoria, W. hanleyi* and *W. lanceolata* it may also be chartaceous or coriaceous apparently due to environmental conditions.

The leaves of *Wrightia* are petiolate or subsessile; the petiole varies in length, ranging from 1 to 10 mm. In the leaf axil usually can be found few to many pectinate glands which may be regarded as intrapetiolar stipules.

Pubescence is variable. *Wrightia hanleyi, W. saligna* and *W. antidysenterica* have glabrous leaves even when immature. The leaves in *W. laevis, W. tinctoria, W. pubescens* and *W. coccinea* are either glabrous or puberulent, whereas those of the remaining species are more or less puberulent, at least along the veins. The degree of pubescence varies greatly even within the species. Leaves may be puberulent only along the veins, especially upon the midrib, on both surfaces or densely puberulent throughout or becoming eventually glabrescent above. In *W. angustifolia* trichomes are confined to the midrib, near the base of the blade, beneath. Finally, *W. sikkimensis* is outstanding for its generally minute puberulence above and its glabrity beneath, except along the veins.

The gross anatomy of the leaf in *Wrightia* offers little variation within the genus. For these studies, portions of leaves from herbarium material were cleared in 5% NaOH, embedded in paraffin according to the tertiary butyl alcohol schedule, sectioned and stained in safranin-fast green combination. As for studies of the leaf epidermis, pieces of entire leaves were cleared and stained with ferric chloride-tannic acid according to Nevling's method (Jour. Arn. Arb. **17:** 295. 1961).

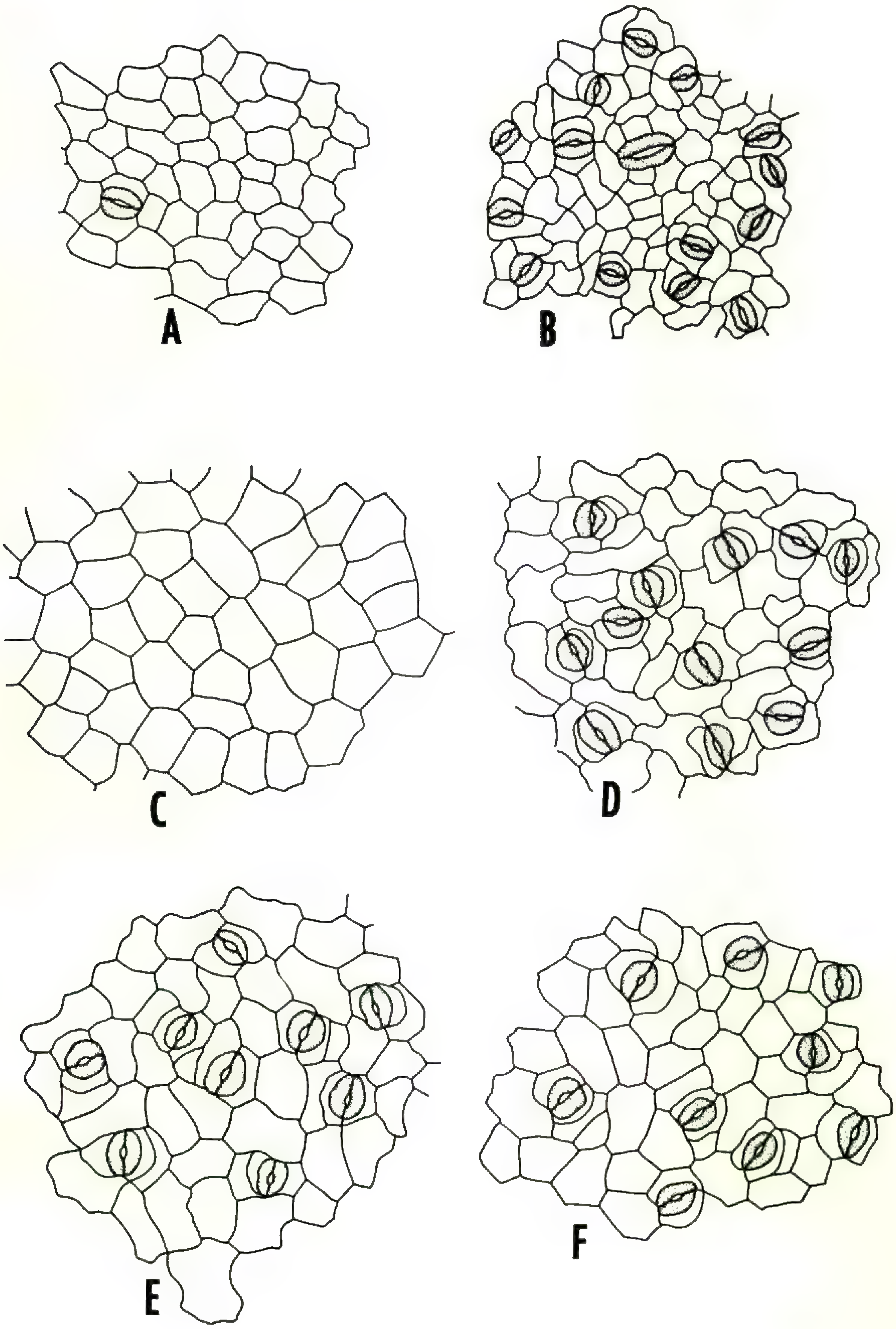
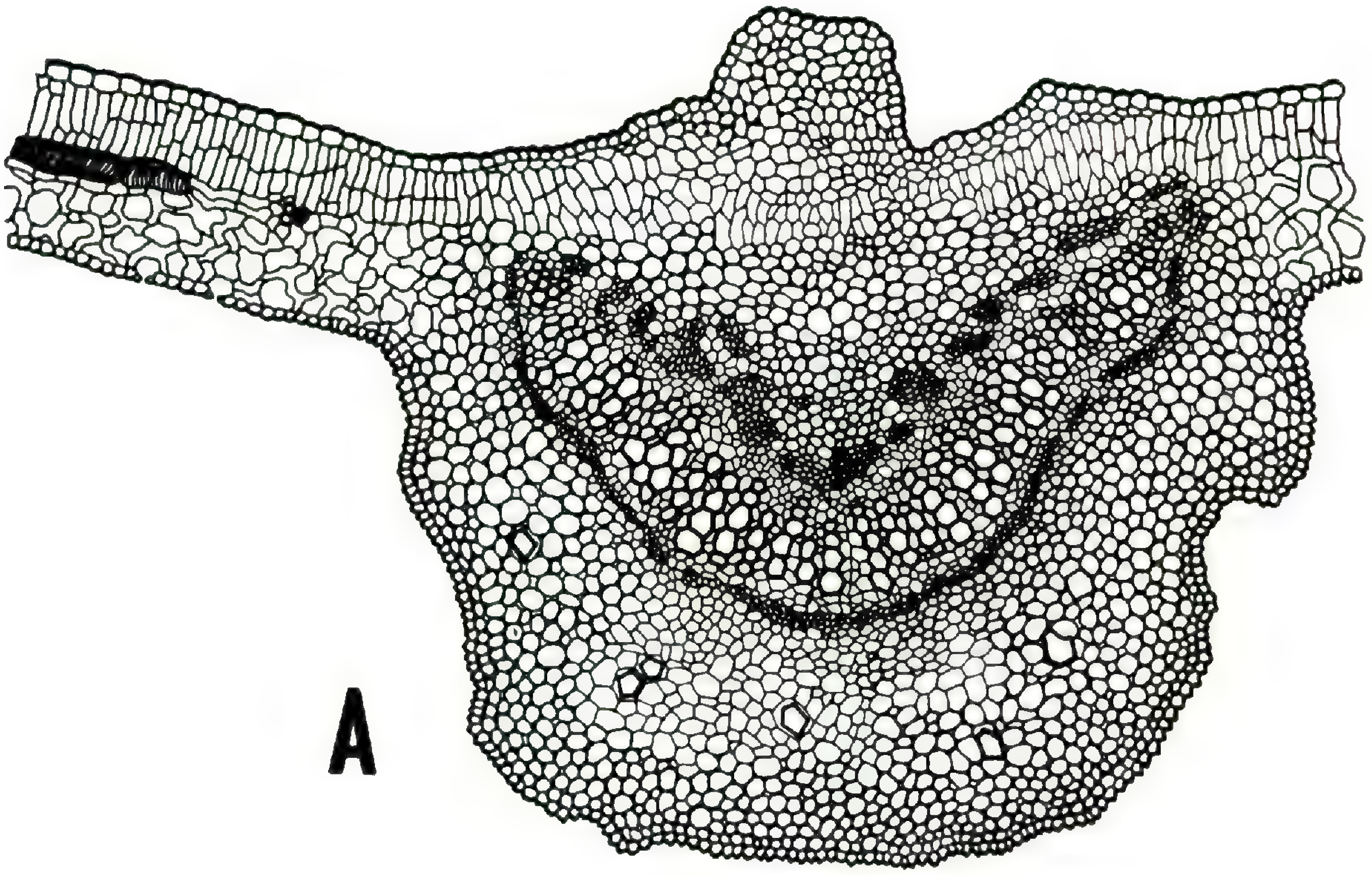


Figure 1. Epidermal structure of leaves of *Wrightia,* adaxial face on the left abaxial face on the right. A-B, *W. laevis* showing scattered stomata on adaxial face and 2 types of stomata on abaxial face; C-D, *W. annamensis;* E-F, *W. saligna* showing stomata on both faces and in approximately equal numbers.



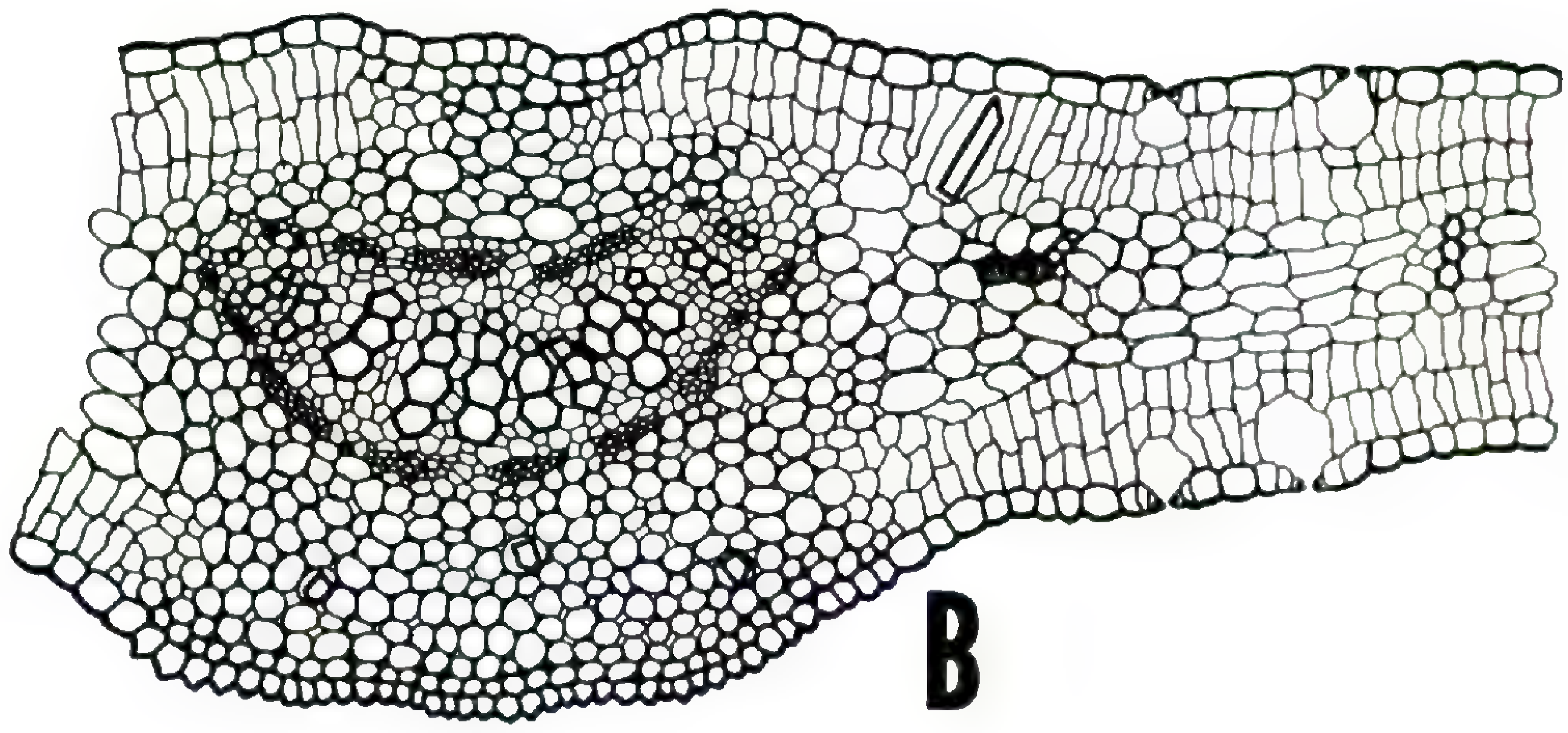


Figure 2. Transections of leaves of *Wrightia*, showing internal phloem and prismatic crystals of calcium exalate. A, *W. annamensis* with a bifacial structure. B, *W. saligna* with an isobilateral structure.

The lamina is typically dorsiventral: the palisade parenchyma is 1-3 layers thick with the cells as long as broad to 3 times as long, and the spongy parenchyma consists of irregular shaped cells. In the mesophyll are found numerous clustered prismatic crystals of calcium oxalate. The petiole in cross section, near the distal end, is provided with a crescentic, median vascular strand and 2 small accessory bundles in the wings, as in *Nerium and Strophanthus* (Metcalfe & Chalk, Anatomy of the dicotyledons **2:** 907. 1950), 2 genera closely related to *Wrightia.* Stomata are of the paracytic type and restricted to the abaxial surface of the leaf; however in some cases they are also found on the adaxial surface but scattered, and this feature appears to have no taxonomic value in *Wrightia.* In many species there are 2 types of stomata on the abaxial surface of the lamina: the paracytic type commonly found in many apocynaceous leaves and a special type with 2 relatively larger guard cells surrounded by 4-8 subsidiary cells (Fig. 1). This feautre aids in the distinction of these species from their related neighbors. Finally, leaves of *W. saligna,* a species endemic to Australia, are notable within the genus in having an isobilateral structure with palisade tissue on both surfaces and spongy parenchyma between; furthermore, stomata are present on both surfaces and in approximately equal numbers (Fig. 2). It is appropriate to mention that *W. saligna* has linear-falcate leaves similar to those of *Eucalyptus* and *Acacia* occurring in this area.

INFLORESCENCE:—The fundamental type of inflorescence in *Wrightia* is a terminal "aggregate dichasium" which consists of a series of dichasia inserted at regular, decussate intervals along the primary axis of the inflorescence. Woodson (Ann. Missouri Bot. Gar. **22:** 1-48. 1935), in a study of the inflorescences of *Apocynaceae,* has pointed out that this type of inflorescence has been derived by the "aggregation of a number of terminal dichasia through the elimination of the foliar nodes subtending them." This reduction is best examplified by many specimens of *W. laevis* and *W. pubescens* in which 1 or both the 2 subsidiary lateral branches accompanying the terminal inflorescence produce, directly, inflorescence without foliage. Different stages of this progression are illustrated in Fig. 3. Evidence of this trend of evolution can also be found in many inflorescences of *W. pubescens, W. coccinea* and *W. puberula* in which bracts retain their foliar character and in certain specimens of *W. pubescens* (*Bur. Sci. 18579, McGregor* A, BM, MS) in which the inflorescences still have foliar nodes.

From the aggregate dichasium, the evolution of the inflorescence in *Wrightia* shows a development towards the cincinnus by reduction of a lateral branch of the dichasium alternately to right and left of the central flower (Fig. 4). The first stages of this development are observable in *W. religiosa* with the branches of the aggregate dichasium having undergone scorpioid modification. The inflorescence consists of the main axis bearing 2 pairs of decussate branches, each of which has become monochasial by the repeated reduction of the right and left branches, alternately, to a solitary flower. Further modifications are found in *W. annamensis* with the suppression of the lateral solitary flowers, and the inflorescence consists of an aggregate of cincinni, or can be reduced to a pair of cincinni borne on a dichasial main axis as in many specimens of *W. dubia* and *W. antidysenterica.*

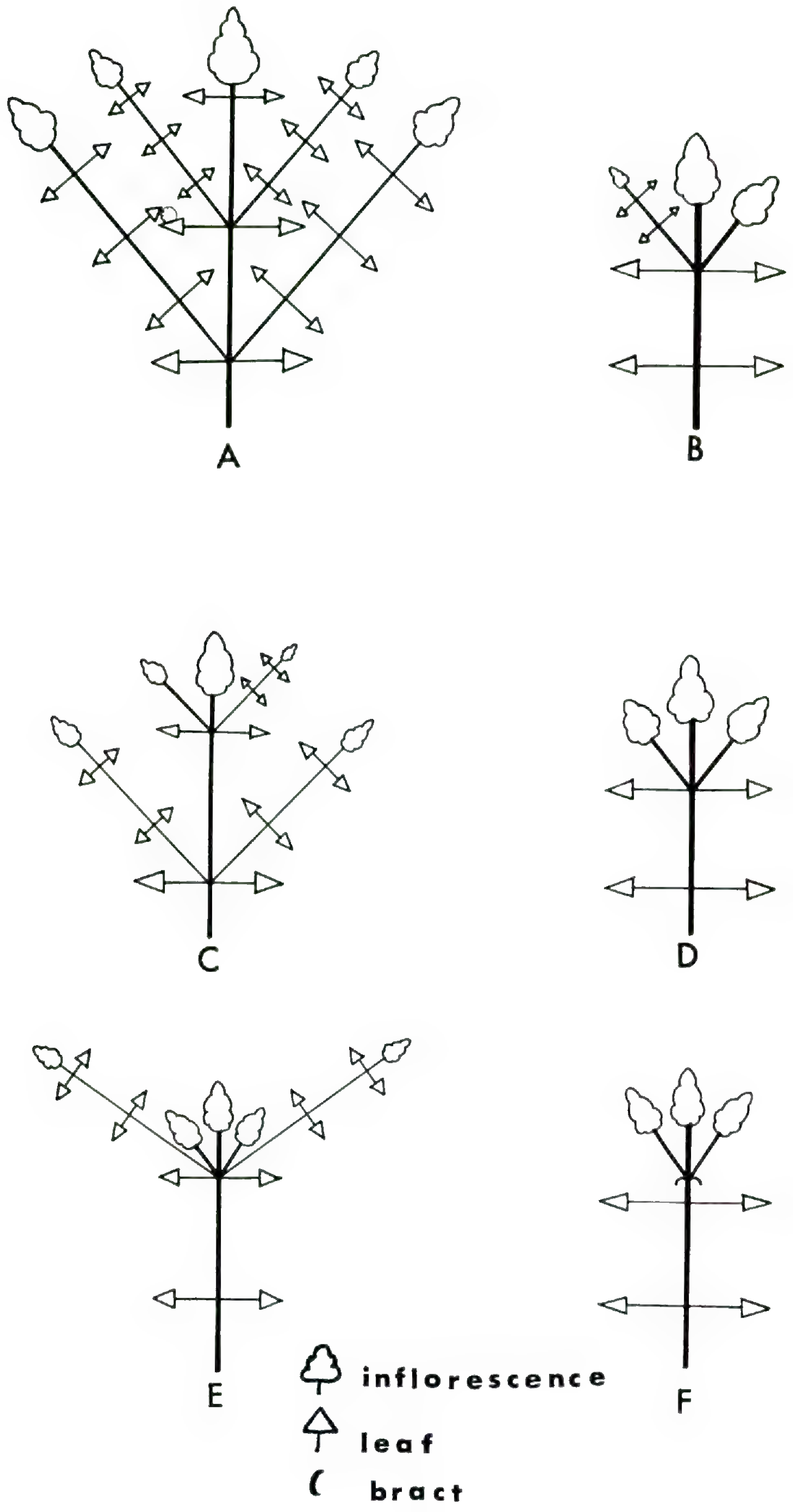


Figure 3. Inflorescence patterns in *Wrightia*. Further explanation in the text.

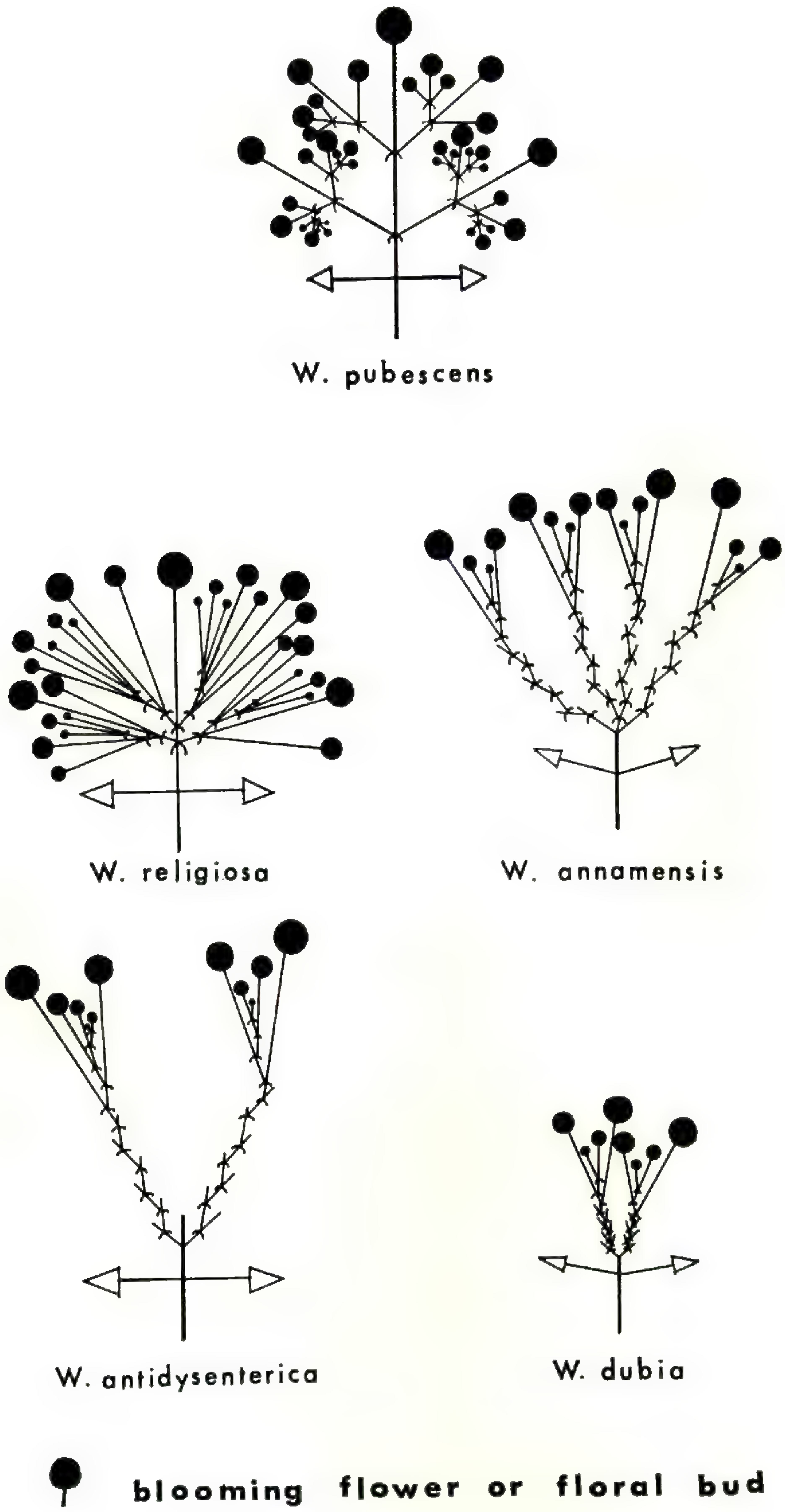


Figure 4. Diagrams illustrating a possible evolutionary trend of inflorescence structure in *Wrightia*. Explanation in the text.

The aggregate dichasia occur throughout the section *Balfouria* and predominate in § *Wrightia* while the cincinni are found in species of § *Wallida* and § *Scleranthera*.

FLOWER: The flower in *Wrightia* is actinomorphic, bisexual and pedicellate; size is variable, ranging from 0.7 cm. long in *W. hanleyi* and *W. viridiflora* to about 5.0 cm. long in *W. antidysenterica*. Flowers of most species are fragrant except those of *W. tomentosa* and *W. viridiflora* which have an unpleasant scent, to judge from the local floras and collectors' notes.

Calyx: The calyx is synsepalous and consists of 5 lobes which are divided nearly to the base and arranged in a quincunx with 2 exterior lobes, 2 interior lobes and an imbricate lobe. The shape and size of the calyx lobes sometimes offer reliable characteristics for the distinction of species or subspecies. For instance, within § *Scleranthera*, the exceptionally long-acuminate lobes of *W. collettii* and some specimens of *W. dubia* are outstanding. On the other hand, *W. coccinea* is readily distinguished from the related species by its caylx lobes relatively large and auriculate.

The calyx bears at the base of the lobes, on the inner face, 5 to many glandular squamellae which can be regarded as the homologues of foliar stipules. Sometimes each lobe is provided with 2 lateral squamellae as in *W. saligna*, but in most cases these are coherent with those of adjacent calyx lobe and thus appear as only 5 alternating ligules confined to the margins of the 2 interior lobes and to the inner margin of the imbricate lobe. The size and shape of the squamellae vary considerably within the genus, but in some instances can be used for the distinction of species. Squamellae are relatively small (about 1/4 the length of the calyx lobe) in *W. coccinea*, *W. hanleyi*, *W. natalensis*, *W. viridiflora* and some specimens of *W. dubia*, whereas in the remaining species they are one-half as long as the calyx or equal to it. Finally, 2 rather closely related species (*W. tinctoria* and *W. laevis*) are easily distinguished by the shape of the squamellae: linear-ovate, acuminate in the former and broadly ovate, acute to serrulate in the latter.

Corolla: The corolla is sympetalous and its shape is a valuable taxonomic criterion of the sections: infundibuliform to subinfundibuliform in § *Scleranthera*, salverform in § *Wallida*, subrotate in § *Wrightia* and subrotate to subsalverform in § *Balfouria*. Coloration may be quite variable within the species and cannot be used in classification derived chiefly from herbarium studies because of changes induced by desiccation as well, perhaps, as inadequacy of sampling. Flowers of *W. tomentosa* have been reported as being variously "yellowish-red," "deep blue-purple," "pale rosy" or "pure white" according to the illustrations and descriptions of various authors. Hooker (Fl. Brit. Ind. **3:** 654. 1882) has remarked on this variability and stated that "there is some obscurity about the colour of the flower of this species, possibly indicating different species or a change during life" or, I might add, the expression of unknown genes affecting pigmentation.

The corolla lobes are sinistrorsely contorted in aestivation and are usually ovate-elliptic to narrowly obovate or oblong-obovate, rarely obliquely ovate or orbicular. The apex is obtuse to acute except in some specimens of *W. dubia* which has narrowly ovate, long-acuminate lobes.

One important feature of the corolla in *Wrightia* is the presence of a corona (except in *W. religiosa*). This is the most variable structure of the flower. The corona is made up of 5 to numerous appendages within the corolla lobes. These appendages are grouped into 3 series: the *antepetalous segments* often strongly adnate to the blade of the corolla lobes except in § *Balfouria*, the *alternipetalous segments* relatively narrower, usually shorter than the antepetalous, and, between these 2 series are found in many species 10 to numerous *alternating supplementary segments* filiform and shorter than the other 2 (except in *W. flavido-rosea*). Some species possess only 1 series of corona segments, either antepetalous or alternipetalous, most of the remaining species have both segments, free from each other or more or less coherent. Finally, other species have all 3 kinds of corona segments. The shape and size of the corona segments vary considerably within the genus, but are constant or show only minor variations within the species. These characters can also be used for the separation of groups within the sections. Coloration of the corona is sometimes different from, or darker than, that of the corolla and may provide a valuable character.

An interesting aspect of the corona is the vascularization of its segments. The antepetalous and alternating supplementary segments are supplied by vacsular bundles from their subtending corolla lobes alone, whilst the alternipetalous segments are vascularized by bundles from both adjacent corolla lobes jointly. Therefore, the 3 series of corona segments are distinct from the stamens and appear to pertain rather to the corolla. The alternipetalous and alternating supplementary segments represent elaborations of the antepetalous, the outermost lateral parts of which are more or less coherent to form the alternipetalous segments. The latter may not develop, as in *W. coccinea* and *W. lanceolata,* or may be minute, as in *W. dubia, W. hanleyi* and *W. pubescens* ssp. *novobritannica.* Finally, in *W. lecomtei* and *W. angustifolia,* the antepetalous segments become obsolete and the corolla retains the alternipetalous segments. In any case, by their position with respect to the corolla lobes, the 3 series of corona segments can be regarded as the homologues of the calycine squamellae and foliar stipules.

Stamens: As in the other genera of the *Echitoideae,* the stamens of *Wrightia* are epipetalous and have the anthers coherent into a cone about the stigma and closely adherent to this organ by means of glandular secretions. Species of § *Scleranthera* have the stamens inserted within the corolla tube from the base to near the orifice, whereas those of the 3 other sections have the stamens inserted at the orifice. Each anther consists of 4 fertile sporangia borne on the upper third of the ventral face of an enlarged sagittate connective; at maturity of the pollen each pair of dorsal and ventral loculae is ruptured, giving the appearance of a bisporangiate anther. The connective is provided at the base with 2 obtuse or narrowly attenuate basal lobes and at the apex with a membranaceous appendage or acumen. The pubescence of the acumen and dorsal face of the connective is also useful for the distinction of the species.

Very few observations concerning the pollen of *Wrightia* have been made. Pichon (Mém. Mus. Natio. Hist. Nat., nouv. sér. sér. B, Bot. **1:** 1-174. 1950), in

his treatment of the *Echitoideae,* merely mentioned that *Wrightia* has 4-porate pollen grains, but did not give the characteristics of the structure. In the present study pollen grains from herbarium material were boiled in water, stored in FAA, then treated with lactic acid and mounted in Hoyer's medium according to Dressler's method (Contr. Gray Herb. **182:** 1-188. 1957). Pollen samples were also prepared by acetolysis (Erdtman, Pollen morphology and plant taxonomy. Stockholm 1952) for comparison.

Pollen grains of all species of Wrightia do not offer great variation. They are 3- to 4-porate, the pores confined to the equator. According to Erdtman's terminology they belong to the category of tri- and tetratreme zonoporate spores. In shape they are oblate. Exine stratification is sometimes obscure; however many pollen samples show distinct structure, with small more or less perpendicular perforations (punctitegillate).

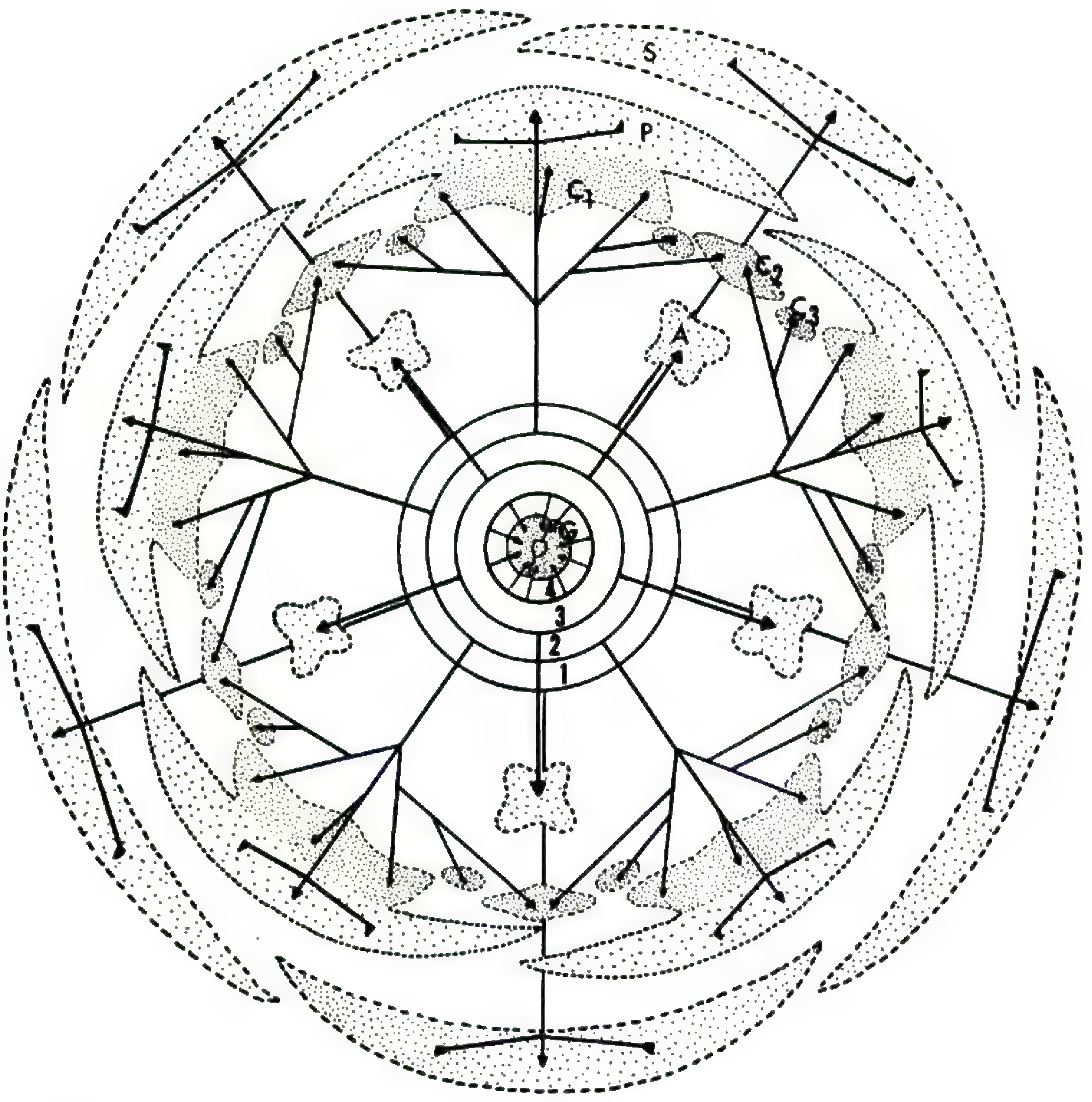


Figure 5. Diagram showing vascular pattern in flower of *Wrightia.* S, calyx lobes, P, corolla lobes, C_1 antepetalous corona segments, C_2 alternipetalous segments, C_3 alternating supplementary segments, A, stamens, G, carpels, 1-4 consecutive residual steles.

Pistil: The pistil is always bicarpellary and superior, the 2 carpels being coherent or free from the base to the common style. Unlike the majority of genera of the *Echitoideae, Wrightia* has the pistil destitute of glandular organs or nectaries surrounding the ovary. The latter is usually glabrous, except in *W. angustifolia* and *W. flavido-rosea* which have the carpels densely pubescent at the top. The common style is columnar, gradually or abruptly dilated near the stigma. The stigma is subcapitate to subcylindrical with a well-developed basal collar to which are appressed the 5 anthers, a constricted median region, and an enlarged distal portion ending in a more or less bi-apiculate apex.

Anatomy of the flower: For this study flowers of *W. pubescens* ssp. *laniti, W. religiosa, W. dubia* and *W. antidysenterica* were sent to me fixed in FAA from Vietnam and Ceylon. They were passed through the usual series of butyl alcohol to paraffin and serial transverse sections were stained with fast green-safranin. Flowers were also cleared whole in lactic acid for comparison.

The vascular anatomy of the flower in species of *Wrightia* thus observed offers a homogeneous pattern which can be summarized in Fig. 5. The pedicel has a bicollateral stele with a number of protoxylem strands embedded in a cylinder of protophloem parenchyma. The stele, at first circular in outline, gradually becomes pentagonal, and each of the 5 angles will supply a calyx lobe. Shortly after leaving the stele, these traces give rise to many laterals upon either side and the calyx lobes are entirely supplied by their own vascular bundles. It is interesting to note that this organization falls into the type III described by Woodson and Moore (Bull. Torr. Bot. Club **65**: 135. 1938) who also found it in species of *Nerium* and *Strophanthus,* 2 genera closely related to *Wrightia.* After the departure of the calycine traces, 10 other traces leave the stele and give rise to the bundles of the corolla lobes and the 5 epipetalous stamens, and in the center of the receptacle a residual stele remains which is destined to supply the walls of the carpels and the ovules. From the residual stele which is roughly circular, at first, then becomes elliptic, 4 equidistant bundles migrate toward the center to become the placental bundles of the 2 carpels.

At the level of the insertion of the stamens, the corolline bundles branch and the laterals furnish traces which enter the corona segments. The antepetalous segments as well as the alternating supplementary segments are vascularized solely by the traces of the subtending corolla lobe, whilst the alternipetalous segments each receive 2 vascular strands from the outermost lateral bundle of each adjacent corolla lobe. Furthermore, within § *Scleranthera,* characterized by the stamens inserted below the orifice of the corolla tube, the corolline bundles give off branches at the level of insertion of the stamens, some supplying the corona segments, whereas in § *Wrightia,* § *Balfouria* and § *Wallida* they divide only at the orifice of the corolla tube. Finally, *W. hanleyi* is outstanding for the appendages within the corolla tube being vascularized by branches descending from the orifice of the tube.

FRUIT. The fruit of *Wrightia* is a pair of pendulous follicles which may be terete-fusiform and free, or laterally compressed along the suture and coherent.

When coherent, they are more or less deeply grooved at the commissure. In some instances at maturity, the free follicles remain coherent at the tip. Their size varies from 10 to 50 cm. long; their color ranges from green-olive to dark green, becoming brown or black in desiccation. The pericarp is glabrous (sometimes minutely puberulent in *W. angustifolia* and *W. flavido-rosea*), more or less striate and often provided with numerous prominent orbicular to ovate-linear lenticels.

Seeds. The seed is linear-fusiform, attenuate at the tips and provided with a basal, therefore, chalazal, coma as determined by the position of the embryo (Fig. 6). The seed coat is coriaceous and easily separable from the scanty and

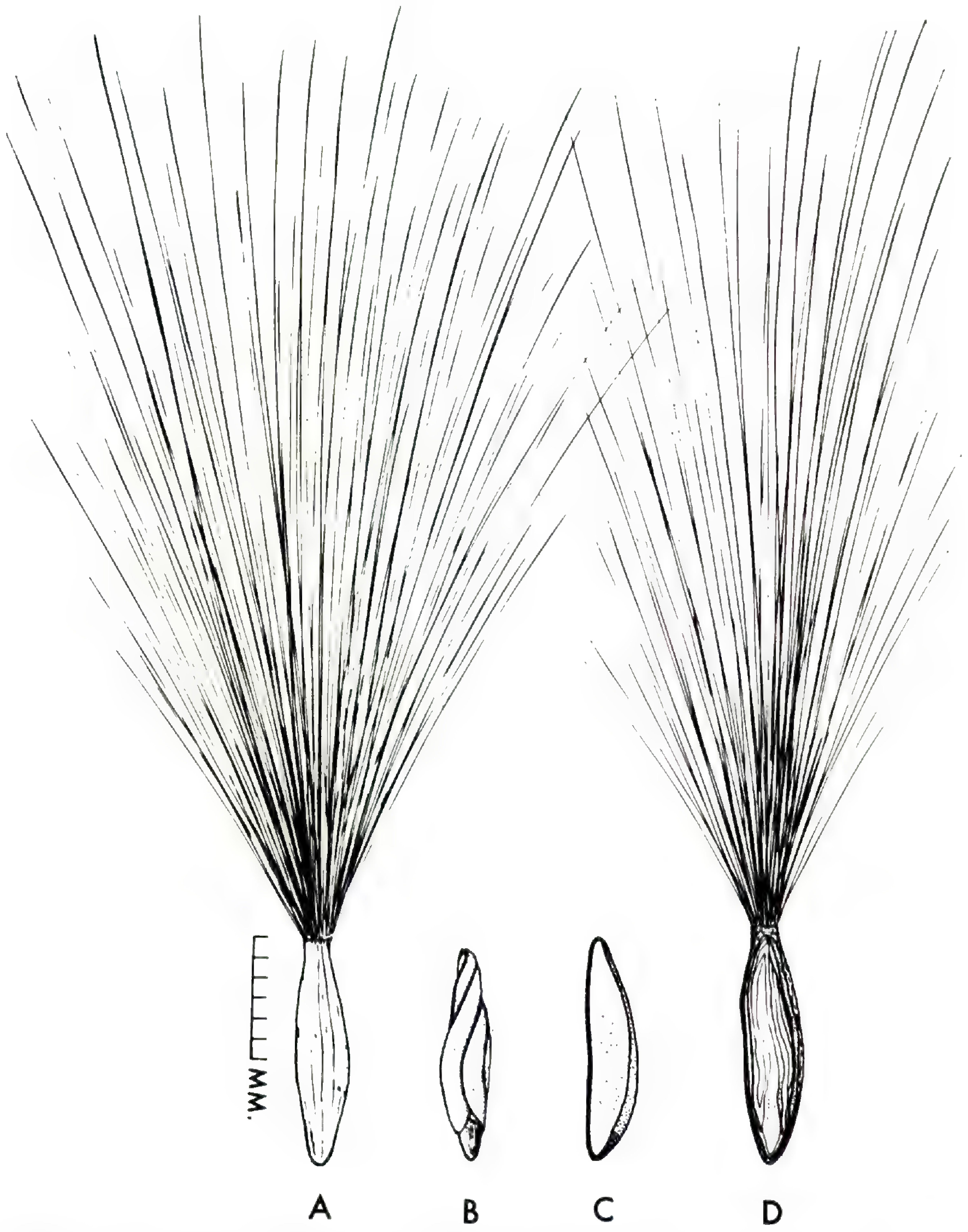


Figure 6. Structure of the seed and embryo of *Wrightia*. A, seed; B, embryo; C, longisection of the endosperm; D, longisection of the seed.

membranaceous endosperm. The embryo is erect and almost as long as the seed, with the cotyledons very broad and convolute. Embryo color ranges from whitish to yellow and reddish.

SPECIFIC CONCEPT

There is considerable confusion with regard to the delimitation of some species in *Wrightia* owing to variability in the taxonomic characters; they are formed by a cluster of variants possessing individual morphological differences which intergrade through numerous intermediates. In the past, many authors have assigned specific rank to such populations. Other authors (Pichon, Not. Syst. **14:** 77. 1951) on the contrary, treat the problem in a very inclusive sense and combine into a single taxon many species which seem to me distinct.

In the present treatment of the genus, special effort was made in an attempt to reach objective criteria which may reveal what a species in *Wrightia* really is. For this purpose I have found the "species—standard" method of Rollins (Rhodora **54:** 1-19. 1952) very stimulating and helpful. Within the genus, *W. laevis* and *W. tinctoria* can be used as "biological standards" of comparison because of the relatively ample specimens of them available to this study; they possess reliable characters to be recognized in spite of variability in the size of leaves and in the structure of the corona.

Size of leaves in *W. laevis* and *W. tinctoria* ranges from about 6 to 18 cm. long and from 2 to 8 cm. broad. Flowers of both species have 3 series of corona segments, more or less fimbriate and subject to great variability. The antepetalous and alternipetalous segments may be deeply laciniate to multifimbriate, the fimbriae simple or variously branched as shown in Fig. 7. However, the 2 species can be distinguished from each other by the relative length of corona segments which appears to be constant: in *W. laevis,* the alternipetalous segments are about as long as the antepetalous and in *W. tinctoria,* they are about half as long. Furthermore the alternating supplementary segments are solitary and simple in the former and geminate, simple or bifid in the latter.

In both species leaves may in general be glabrous, even when immature, or minutely puberulent on the lower surface especially along the midvein, or densely puberulent on both surfaces. However, in *W. tinctoria,* leaves are short-petiolate or subsessile with 9-13 pairs of secondary veins, while in *W. laevis* they are long-petiolate with usually 6-9 secondary veins. Finally, the calycine squamellae are linear-ovate, acuminate in the former and broadly ovate, acute to serrulate in the latter. In brief, in spite of the apparent similarity in leaf shape and size, and in corona structure, the 2 species are quite distinct in the relative length of the corona segments. This distinction is reinforced by characters of leaf and squamellae.

The variability in leaf pubescence, corona structure and other floral structures observed within *W. laevis* and *W. tinctoria* provides the basis for interpreting the remaining taxa of *Wrightia.* From this standpoint, I believe that *W. cambodiensis* and *W. rubriflora* are variants of *W. dubia* and that *W. hainanensis,* on the one hand, and *W. stellata* and *W. schlechteri,* on the other hand, should be put in synonymy under *W. laevis* and *W. sikkimensis,* respectively. Yet, *W. laevis* and

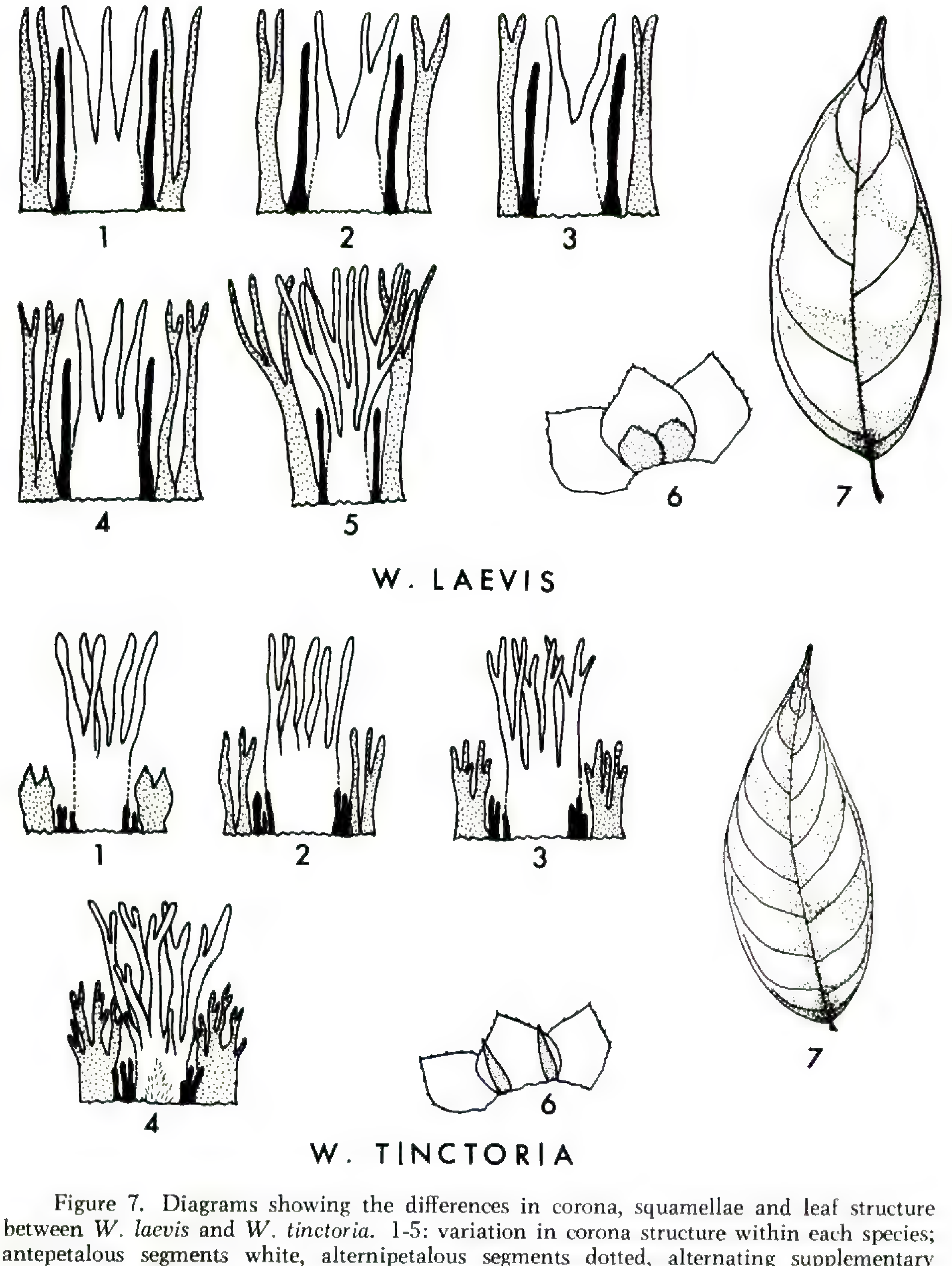


Figure 7. Diagrams showing the differences in corona, squamellae and leaf structure between *W. laevis* and *W. tinctoria*. 1-5: variation in corona structure within each species; antepetalous segments white, alternipetalous segments dotted, alternating supplementary segments solid black; 6: calyx lobes and squamellae; 7: leaf.

W. sikkimensis are definitely distinct from *W. tinctoria* and *W. pubescens*, respectively. *Wrightia flavido-rosea* has been treated by Pichon (Not. Syst. **14**: 77. 1951) as a synonym of *W. pubescens.* However, on the basis of corona structure, *W. flavido-rosea* is more closely related to *W. laevis*, from which it differs in that alternating supplementary corona segments are as long as the other segments. This distinction is substantiated by the fact that in *W. flavido-rosea* the carpels are densely pubescent at the tip, the follicles coherent and the leaves sparsely puberulent on both surfaces. There can be little doubt that this species should be maintained as distinct. *Wrightia lanceolata* should also be regarded as distinct from *W. tomentosa* for it is devoid of alternipetalous segments.

Finally, *W. puberula* has been put in synonymy under *W. tinctoria* or *W. flavido-rosea.* However, it differs from the former in the alternipetalous segments as long as the antepetalous, the absence of alternating supplementary segments, the leaves sparsely puberulent on both surfaces and, from the latter, in the absence of supplementary segments and the glabrous carpels. Therefore, *W. puberula* is treated in this revision as a distinct species even upon the basis of a single collection.

GEOGRAPHICAL DISTRIBUTION

Wrightia is confined to the eastern hemisphere, from East Africa to the Solomon Islands and from India and southern China to northeastern Australia. Within these bounds, species of *Wrightia* occur between the latitudes of about 30° N. and 30° S; altitudinally they range from sea level to about 1800 m. Their habitats are quite varied, from rain forests, deciduous dry forests to steppes, savannas and sandy thickets on the strand.

The largest section, *Wrightia*, embraces the whole range of the genus except Africa; there are 4 species with relatively extended ranges. The widespread species *W. laevis* and *W. pubescens* occur from southern China to northeastern Australia through Indochina, Thailand, Malaya, Indonesia, the Philippines and New Guinea. *Wrightia tomentosa* centers in India and extends to Ceylon and adjacent China, Burma and Thailand while *W. tinctoria* is confined to India . The remaining species of this section are rather local and endemic; for instance, *W. angustifolia*, *W. flavido-rosea* and *W. puberula* are restricted to Ceylon, *W. lanceolata* and *W. viridiflora* to Thailand, *W. lecomtei* to Thailand and Cambodia, *W. kwangtungensis* to Kwangtung and northern Vietnam, *W. annamensis* to Vietnam.

Species of § *Balfouria* are scattered and very limited in distribution. There are 2 species known only from East Africa: *W. demartiniana*, which frequents the wooded steppe, is found in Somalia and adjacent Ethiopia and Kenya, and *W. natalensis* is endemic to Natal. Finally, the third species of this section is restricted to northern Australia.

Section *Wallida* with one species, *W. antidysenterica*, is endemic to Ceylon.

The 4 species of § *Scleranthera* are also more or less limited in their geographical ranges: *W. dubia* covers Malaya, Thailand, Cambodia and South Vietnam, *W. collettii* is confined to Burma, *W. coccinea* is restricted to eastern India and Yunnan, while *W. hanleyi* is endemic to Palawan Island in the Philippines.

Since the majority of species, including many very restricted endemics, are found in the area between India and Southern China, I infer that the center of dispersal of the species is probably located there.

ECONOMIC USES

There are few available records of economic uses for *Wrightia*. Certain members of the genus, *W. pubescens*, *W. laevis*, *W. tomentosa* and *W. tinctoria*, include small or medium-sized trees which are usually classified as a timber for local purposes. The wood is light, soft and fine-textured, hence suitable for carving and turnery. Detailed accounts of the wood anatomy of these species are found in studies by Pearson and Brown (Commercial timbers of India. Calcutta. 1932) and by Ingle and Dadswell (Austral. Jour. Bot. **1:** 10. 1953).

Other species have ornamental value: *W. religiosa* and *W. antidysenterica* are widely cultivated for their beautiful and fragrant white flowers. Species of *Wrightia* have been used to a limited extent by the native population for their chemical and medicinal properties. The seeds, roots and leaves of *W. tinctoria*, *W. tomentosa* and *W. dubia* furnish an indigo-yielding glucoside used for dyeing in India and Cambodia. In India, Cowen (Flowering trees and shrubs in India. Bombay. 1911) states that the sap of *Wrightia tinctoria* has an interesting preservative property since "if a few drops of sap are added to milk, the milk will remain fresh without the necessity of keeping it on ice, the taste remaining unaltered." The bark and seeds of this species have also been used against dysentery and miscellaneous ills (Chopra, R. N., S. L. Nayar, and I. C. Chopra. Glossary of Indian medicinal plants. New Delhi. 1956). Duthie (Fl. Upper Gangetic Plain. Calcutta. 1911) reports that in India "the bark of the stem and root of *W. tomentosa* is regarded as an antidote to snake bite and the sting of scorpions."

ACKNOWLEDGEMENTS

I am indebted to the Agency for International Development (A. I. D.) for sponsoring my visit to the United States and for the award of the scholarship which enabled me to undertake this investigation. I wish to thank Dr. F. W. Went, former director of the Missouri Botanical Garden, where this study was completed, for the privilege of using the library and herbarium. I would also like to thank Mr. M. A. Jayaweera, director of the Botanic Garden in Peradeniya (Ceylon), Messrs. Nghiem song Ho and Ly van Hoi of the Botany Dept., University of Saigon for providing preserved flowers for anatomical studies, Miss D. Helmich of the Pollen Laboratory (Dept. of Botany), University of Michigan for preparing a number of pollen samples by acetolysis. Sincere appreciation is extended to Dr. A. Robyns, Dr. G. B. Van Schaack, Dr. J. Duke and Dr. R. L. Dressler for their encouragement and aid during the course of this study. Finally, I am especially grateful to the late Professor R. E. Woodson, Jr. for his constant interest, his valuable guidance and constructive criticism.

For the loan of material from the following herbaria I express my thanks to their curators for the generous loans of material necessary for this investigation.

The abbreviations are from the Index Herbarium, ed. 4, 1959, excepting SAIG which refers to the Directorate of agricultural research, Ministry of Rural Affairs, Saigon, Vietnam. These include: A, BM, BRI, CAL, CANB, E, EA, F, FI, G, GH, HK, K, L, LAE, MEL, MICH, MO, NSW, NT, NY, P, PH, PRE, SING, SRGH, UC, UPS, US, W.

TAXONOMY*

WRIGHTIA R. Br., Mem. Wern. Soc. **1**: 73. 1811; Tsiang, Sunyatsenia **4**: 42. 1939; Pichon, Not. Sys. **14**:77. 1951, non Solander ex Naudin (1852). (T.: *W. pubescens* R. Br.)

Balfouria R. Br., Mem. Wern. Soc. **1**: 70. 1811. [T.: *B. saligna* R. Br. ex A. DC]
Anasser, Blco. Fl. Filipp. 112. 1837, non. Jussieu. [T.: *A. laniti* Blco.].
Piaggiaea Chiov. Fl. Som. **2**: 290. 1932. [T.: *P. demartiniana* Chiov.].
Wallida Pichon, Not. Syst. **14**: 87. 1951. [T.: *W. antidysenterica* (L.) Pichon].
Scleranthera Pichon, loc. cit. 88. 1951. [T.: *S. cambodiensis* (Pierre) Pichon].

Laticiferous shrubs or trees, occasionally climbers, evergreen or deciduous. Leaves decussate, simple, entire, penninerved, eglandular, the petiole bearing in the axils few to numerous pectinate glands. Inflorescence terminal, aggregate dichasial or monochasial, few- to many-flowered; calyx 5-parted, the lobes equal to subequal, quincuncial, cleft nearly to the receptacle, bearing within 1-2 alternate, glandular squamellae; corolla subrotate to subinfundibuliform, occasionally infundibuliform, subsalverform and salverform, the tube cylindrical to campanulate, constricted or not at the orifice, sometimes annulate, rarely appendaged within, the limb actinomorphic, 5-parted, sinistrorsely contorted in aestivation; corona (absent in *W. religiosa*) of 5-many subentire, dentate, laciniate or fimbriate segments, distinct or coherent; stamens 5, inserted within the corolla tube or at the orifice, the anthers included to wholly exserted, connivent and agglutinate to the stigma, consisting of 4 reduced fertile sporangia borne ventrally at the upper third of an enlarged sagittate connective; carpels 2, coherent or free from the base to the common style, glabrous or occasionally pubescent, the style gradually dilated near the apex and surmounted by a subcapitate to subcylindrical stigma provided with a basal collar and a bi-apiculate apex; nectaries none. Follicles 2, free or coherent, terete to laterally compressed, dehiscing along the ventral suture; seeds numerous, linear-fusiform with a chalazal coma; embryo straight, the cotyledons broad, convolute.

KEY TO THE SECTIONS

a. Corolla subrotate, occasionally subsalverform or salverform; stamens inserted at the orifice of the corolla tube (except in *W. annamensis*), the anthers exserted; inflorescence aggregate dichasial rarely monochasial.
  b. Corolla subrotate (subsalverform in *W. demartiniana*), the tube relatively stout, shorter than the lobes, 1.5-7.0 mm. long, glabrous within; corona glabrous within, occasionally pubescent; anthers frequently pubescent without, sometimes glabrous, the basal lobes attenuate to auriculate, as

* Because of space limitations a list of exsiccatae has not been included in this paper, but a mimeographed copy is available from the author upon request.—*Editor.*

long as or shorter than the filament; leaves puberulent at least upon the veins beneath, rarely glabrous.

c. Corona segments free or merely coherent at the very base (except in in *W. tomentosa* ssp. *pauciflora*), the antepetalous, when present, strongly adnate to the blade of the corolla, 3-7 mm. long. Plants of tropical Asia and Australia .... 1. WRIGHTIA

cc. Corona segments more or less coherent about the stamens, the antepetalous merely adnate to the base of the corolla lobes, 1.0-2.5 mm. long. Plants of Africa and Australia .... 2. BALFOURIA

bb. Corolla salverform, the tube slender, longer than the lobes, 17-28 mm. long, puberulent within; corona minutely puberulent within; anthers glabrous without, the basal lobes attenuate, longer than the filament; leaves glabrous even when immature. Plants of Ceylon .... 3. WALLIDA

aa. Corolla infundibuliform to subinfundibuliform; stamens inserted within the corolla tube, the anthers completely included to more or less exserted; inflorescence monochasial rarely few-flowered, aggregate dichasial. Plants of Asia .... 4. SCLERENTHERA

SECTION 1. WRIGHTIA

§ *Bammatophyton* A. DC. in DC. Prodr. **8:** 404. 1844.
§ *Gymnowrightia* K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. **4**(2): 183. 1895.

KEY TO THE SPECIES

a. Antepetalous corona segments present; stamens relatively stout, the basal anther lobes auriculate, occasionally attenuate, the filament relatively short and stout; calycine squamellae ovate to broadly ovate or deltoid, rarely narrowly ovate; follicles free or coherent.

b. Corona of 3 series, both antepetalous and alternipetalous together with alternating supplementary segments, the antepetalous segments more or less laciniate to fimbriate; follicles free, terete, rarely coherent.

c. Flowers relatively slender, 0.7-1.7 cm. long; corolla tube cylindrical, 1.5-3.0 mm. long; carpels free, rarely coherent.

d. Alternipetalous corona segments ⅔ to as long as the antepetalous, the alternating supplementary segments solitary and simple; calycine squamellae deltoid-ovate to broadly ovate, acute to serrulate.

e. Carpels free from the base to the common style; follicles free; calycine squamellae broadly ovate, acute to serrulate; leaves glabrous above, occasionally puberulent upon the veins.

f. Inflorescence usually many-flowered; flowers fragrant, relatively large, 1.0-1.7 cm. long; alternipetalous corona segments about as long as the antepetalous; anthers puberulent, rarely glabrous without, the acumen glabrous to barbate; leaves usually with 6-9 pairs of secondary veins, glabrous to puberulent upon the veins beneath .... 1. W. LAEVIS

ff. Inflorescence few-flowered; flowers malodorous, relatively small, about 0.7 cm. long; alternipetalous corona segments about ⅔ as long as the antepetalous; anthers glabrous without, the acumen glabrous; leaves with 9-12 pairs of secondary veins, glabrous except upon the veins to densely puberulent beneath .... 2. W. VIRIDIFLORA

ee. Carpels medially coherent along the commissure; follicles coherent; calycine squamellae deltoid-ovate; leaves puberulent above.

g. Carpels densely pubescent at the apex; alternating supplementary corona segments as long as the other 2, the antepetalous fimbriate and as long as the alternipetalous; leaves narrowly elliptic to narrowly ovate ....3 W. FLAVIDO-ROSEA

gg. Carpels glabrous; alternating supplementary corona segments shorter than the other 2, the antepetalous laciniate and longer than the alternipetalous; leaves elliptic to ovate .... 4. W. INDICA

dd. Alternipetalous corona segments ⅓ to about half as long as the antepetalous, the alternating supplementary segments geminate, simple to compound; calycine squamellae narrowly ovate to linear, acuminate .... 5. W. TINCTORIA

cc. Flowers relatively stout, about 2 cm. long; corolla tube campanulate, about 4 mm. long; carpels coherent .... 6. W. KWANGTUNGENSIS

bb. Corona without alternating supplementary segments (except in few specimens of *W. tomentosa* and *W. pubescens*), the antepetalous segments subentire, crenulate or dentate (laciniate in *W. puberula*); follicles coherent, compressed laterally along the commissure (free in *W. sikkimensis*).

h. Leaves membranaceous; alternipetalous corona segments present, the antepetalous more or less free from the corolla lobes; current season's branchlets terete to compressed.

i. Antepetalous corona segments laciniate; calycine squamellae deltoid-ovate, acute .... 7. W. PUBERULA

ii. Antepetalous corona segments dentate, crenulate or subentire; calycine squamellae ovate, broadly ovate to orbicular, acute to serrulate.

j. Follicles free; corolla tube about 2 mm. long; antepetalous corona segments subentire, relatively narrow, about ⅓ the width of the corolla lobe .... 8. W. SIKKIMENSIS

jj. Follicles coherent; corolla tube about 4 mm. long; antepetalous corona segments dentate to crenulate, occasionally subentire, relatively broad, half to ¾ the width of the corolla lobe.

k. Flowers malodorous; corona ½ to ⅔ as long as the stamens, glabrous within, the antepetalous segments with about half their length adnate to the corolla lobes, relatively broad, frequently overlapping the broad alternipetalous and about as long .... 9. W. TOMENTOSA

kk. Flowers fragrant; corona usually about as long as the stamens, glabrous to pubescent within, the antepetalous segments medially adnate to the corolla lobes (half adnate in *W. pubescens* ssp. *penicillata*), relatively narrow, much longer than to almost as long as the narrow alternipetalous.

l. Inflorescence aggregate dichasial, 40-60-flowered; stamens inserted at the orifice of the corolla tube, the anthers completely exserted; leaves minutely puberulent to densely pubescent .... 10. W. PUBESCENS

ll. Inflorescence monochasial, 10-40-flowered; stamens inserted more or less within the corolla tube, the anthers more or less exserted; leaves minutely puberulent along the veins, beneath .... 11. W. ANNAMENSIS

hh. Leaves chartaceous to coriaceous; alternipetalous corona segments obsolete, the antepetalous completely adnate to the corolla lobes; current season's branchlets more or less angular .... 12. W. LANCEOLATA

aa. Antepetalous corona segments obsolete; stamens relatively slender, the basal anther lobes slenderly attenuate, the filament relatively long and slender; calycine squamellae linear-lanceolate to narrowly ovate, rarely ovate; follicles free.

m. Inflorescence aggregate dichasial; corona present.

n. Leaves linear-elliptic to linear-ovate, glabrous except upon the midrib beneath; flowers about 0.8 cm. long; corona about 5 mm. long; carpels densely pubescent at the apex .... 13. W. ANGUSTIFOLIA

nn. Leaves elliptic, minutely puberulent throughout; flowers about 1.8 cm. long; corona minute, about 1 mm. long; carpels glabrous ......14. W. LECOMTEI

mm. Inflorescence monochasial; corona obsolete ......15. W. RELIGIOSA

1. WRIGHTIA LAEVIS Hook. f. Fl. Brit. Ind. **3:** 654. 1882. (T.: *Maingay 1065!*).

Wrightia tinctoria var. *laevis* (Hook. f.) Pichon, Not. Syst. **14:** 80. 1951.

Trees sometimes reaching a height of 35-40 m.; branchlets terete, striate and lenticellate, the current year's growth glabrous. Leaves narrowly elliptic to elliptic, occasionally ovate or obovate, acuminate to caudate-acuminate, rarely mucronate, the base acute, 7-18 cm. long, 2.5-8.0 cm. broad, membranaceous, glabrous to minutely puberulent along the veins beneath, the midrib canaliculate above, prominent beneath, the secondary veins 6-9(-11) pairs, arcuate towards the margins; petiole 0.5-1.0 cm. long, glabrous to puberulent. Inflorescence terminal, aggregate dichasial, usually many-flowered, shorter than the subtending leaves; peduncle about 1 cm. long, glabrous to puberulent, the bracts small, scarious, occasionally linear and foliaceous; pedicels 1.0-1.5 cm. long, glabrous to puberulent. Flowers white to pale yellow, fragrant; calyx lobes ovate to broadly ovate, acute to obtuse, 1-2 mm. long, ciliate, glabrous or puberulent, bearing within 5 ovate to broadly ovate, acute to serrulate squamellae shorter than the lobes; corolla subrotate, the tube cylindrical, relatively slender, 1.5-3.0 mm. long, the lobes narrowly obovate to obovate, 5.5-13.5 mm. long, puberulent-papillate; corona fimbriate, shorter to longer than the stamens, glabrous, the antepetalous segments strongly adnate to the corolla lobes, the fimbriae simple to compound, the alternipetalous as long as the antepetalous, the alternating supplementary segments solitary, filiform and shorter; stamens 5, inserted at the orifice of the corolla tube, the anthers puberulent throughout, occasionally glabrous without, the acumen glabrous to puberulent, the filament longer than the basal anther lobes; carpels 2, free, glabrous, rarely minutely puberulent at the tips, the style slender, dilated near the subcapitate stigma. Follicles 2, free, sometimes coherent at the tips, terete-fusiform, 20-35 cm. long, lenticellate and finely striate; seeds linear, about 2 cm. long, the white coma about 4 cm. long.

Widely distributed in southern China, Burma, Thailand, Indochina, Malaya, Indonesia, Philippines, New Guinea and northern Australia, in evergreen forests, secondary forests and sandy thickets on the strand; flowering from April to July, fruiting from September to January.

Vernacular names: *Lam muk* (China - Lei); *Lam shue* (China - Lei); *Shan Lam shue* (China - Tsang); *Lanete* (Philippines - Sulit).

KEY TO THE SUBSPECIES

a. Corona about as long as the stamens, the fimbriae simple; carpels glabrous.

b. Inflorescence glabrous. Plants of China, Burma, Thailand, Indochina, Malaya and Sumatra ......1a. W. LAEVIS SSP. LAEVIS

bb. Inflorescence puberulent. Plants of the Philippines, Indonesia, New Guinea and Australia ......1b. W. LAEVIS SSP. MILLGAR

aa. Corona definitely longer than the stamens, the fimbriae compound; carpels glabrous to very minutely puberulent at the apex. Plants of New Guinea. ......1c. W. LAEVIS SSP. NOVOGUINEENSIS

1a. WRIGHTIA LAEVIS ssp. LAEVIS

Wrightia hainanensis Merr. in Philipp., Jour. Sci. **21**: 352. 1922. (T.: *Hongkong Herb. 425*).
Wrightia balansae Pitard in Lecomte & Humbert, Fl. Gen. Indo-Chine **3**: 1188. 1933. (T.: *Balansa 2118!*).
Wrightia macrocarpa Pitard in Lecomte & Humbert, loc. cit. 1190. 1933. (T.: *Balansa 2115!*).
Wrightia hainanensis var. *variabilis* Tsiang, Sunyatsenia **4**: 47. 1939. (T.: *Tsiang 2679!*).
Wrightia hainanensis var. *chingii* Tsiang, loc. cit. 48. 1939, ex char. (T.: *Ching* 5539).

BURMA. S. E. SHAN STATES: Keng Tung Territory, *Rock s. n.* (A).

CHINA. HAINAN: Fan Ya, Ng. Chi Leng, in forested ravine, *Chun & Tso 44159* (A, NY), *McClure 9488* (UC, US, W); Five Finger Mt., *McClure* 8685 (A, BM, E, G, HK, K, MO, UC), *Chun 1528* (UC); Hoi ta Shan, Taam Chau distr., *Tsang* 823 (A, G, K, NY, UC, US); Hung mo Shan, Lai area, *Tsang, Tang & Fung 174* (BM, G, K, NY, US), *Tsang & Fung 628* (NY); Lokwei, in forest, *How 72313* (BM, F); Pak shik Ling and vicinity, Ching Mai distr. in thicket on sandy soil, *Lei 233* (A, K, NY, SING, UC, US, W), 565 (A, HK, L, NY, SING, UC, US, W); Poting, *How 71703* (A, G), 73280 (A, BM, G); Sha Po Shan, Taam Chau. distr., *Tsang 582* (A, K, UC, US); Tai pin, edge of jungle, *Gressitt 1073* (A, BM, E, G, MO); Tong mok Sze, *Ford 425* (K); Tsat cha ling, Chang kiang distr., *Lau 1761* (A, BM, NY); precise locality unknown, *Liang* 63443 (NY, US), 63637 (A, NY), *65059* (A, G, NY), *Tang 412* (A). HONGKONG: Botanic Garden, *Tang* 33 (HK), *100* (HK); Kaepong, *unknown collector 446* (HK). KWANGSI: Mung Tung Kow, 65 mi. N. of Luchen, in woods, *unknown collector* 5539 (W); Nar Pui, Sup Man Ta Shan, in shaded and mixed woods along the stream side, *Liang* 69588 (A); on the way to Suan Tze, from Nanning, in open wood, *Ching 7768* (A, NY, UC, US, W). KWANGTUNG: Taiping tseh, Sunyi in open, bank of river, *Tsiang 2679* (A, K, NY, W). YUNNAN: Szemao, *Henry 12393* (A, NY), *12743* (A, E, NY).

INDONESIA. SUMATRA: vicinity of Loemban Ria, Asahan, *Rahmat si Boeea s. n.* (A); by river Moesi near Lampar, *Forbes 2605* (BM, CAL, K).

LAOS: Pak Munung, Wiengchan, in evergreen forest, *Kerr 21209* (BM, K).

MALAYA. KELANTAN: Goa Panjang at Goa Ninik, *Henderson 19599* (BRI, SING). MALACCA: Mt. Ophir, *Maingay 1065* (CAL, K). NEGRI SEMBILAN: Johol, *Ridley s. n.* (K, SING); Ulu Pedas, *Nur 11728* (SING, UC). PAHANG: near Batu Balai, *Burkill & Haniff 15826* (SING). PERAK: Merah, *Ridley s. n.* (SING); Ulu Temengor, *Ridley 14605* (BM, SING); precise locality unknown, *Scortechini 63b* (CAL), *77b* (CAL, K, SING), WRAY *3504* (CAL). SELANGOR: Bukit Lagong Forest reserve, Kepong, *Sinclair SFN 40103* (BM, E, L, SING); Ginting Bidai, *Ridley 7566* (CAL, SING); Seminyih, *Hume 8352* (SING); near Ulu Selangor, *King 8614* (BM, CAL, L, UC).

THAILAND: NAKAWN SRITAMARAT: Kao Luang, *Kerr 15568* (BM, E, L). PUKET: Bangto, Pang-nga, in evergreen forest, *Kerr 17148* (A, BM, E, L); Pang-nga, *Curtis 2943* (K. SING).

VIETNAM: Hācói, Taai Wong Mo Shan & vicinity, *Tsang 27334* (A); Phútho, *Fleury 30105* (P); Sontây, Mt. Bavī, *Pételot 2429* (A, MO, US), *7018* (MO); Sontây, valley of Lankok, *Balansa 2117* (K, L, P); Tháinguyên, Lang Hit, *Pételot 7008* (MO, SAIG, US); Thanhhóa, Lahán, *Poilane 1722* (A, SAIG); Tupháp, *Balansa 2115* (K), *2118* (K, L); Yên báy, *Pham ngoc Dung 15* (SAIG); precise locality unknown, *Bon 5418* (P), *6057* (P, SAIG), *s. n.* (A, NY).

1b. WRIGHTIA LAEVIS ssp. **MILLGAR** (F. M. Bailey) P.t. Ngan, stat. nov.

Wrightia millgar F. M. Bailey, Dept. Agric. Brisbane, Bot. Bull. **7**: 65. 1893. (T.: *Cowley 7D!*).
Wrightia sorsogonensis Elmer, Leafl. Philipp. Bot. **10**: 3698. 1939. (T.: *Elmer 15595!*).

AUSTRALIA. QUEENSLAND: Barron River, *Cowley 7D* (BRI); Daintree River, *Cowley s. n.* (BRI), *Kajewski 1409* (A, BRI, NSW, NY); near Rockhampton, *Webb 5057* (CANB); Yungaburra, *Michael* 334 (BRI, GH).

INDONESIA. SUMATRA: Moesi, Palembang, *unknown collector s. n.* (L); Tandjong Ning, Palembang, *Forbes 2766* (BM, GH, L, MO, SING). WEST IRIAN: Subdistr. Manokwari, Momi, in primary forests, rare, *Kostermans 256* (L, SING); Subdistr. Manokwari, Ransiki, in primary forests on flat stony and sandy ground, *Kostermans 100* (L); plateau north of Pami River, 8 km. N.W. of Manokwari, in primary forests on coral lime, *Koster BW 4349* (CANB), *BW 4355* (CANB, L, LAE); Sansapor, Onderafd. Sorong, in primary forests, *Versteegh BW 3991* (L, LAE), *BW 4628* (L); Sekoli plain, in secondary forests on stony clay *Iwanggin BW 9136* (LAE); Seroei, Japen Island, F. R. I. *bb 30391* (L.), *bb 30417* (L), *bb 30447* (SING), *bb 30530* (A, L, SING); Tiporra, Rijklof van Goens Bay, Subdiv. Fak Fak, *Stefels BW 5105* (L); Wersar, in primary forest on clayey soil, *Versteegh BW 4971* (L.).

NEW GUINEA. Madang subdistr., Ramu valley about 5 miles S.E. Faita airstrip, in rain forests on lower slopes, *Saunders 484* (BRI, CANB, LAE), *505* (BRI, CANB, LAE).

PAPUA: Buna Hinterland, about 7 miles N. W. of Embi Lake, in rain-forest, *Smith 1272* (L, LAE); Tufi subdistr., near Koreaf village, in dense, tall, partly secondary forest, *Hoogland 4840* (A, BM, BRI, CANB, G, L, LAE, US).

BISMARCK ARCHIPELAGO: Admiralty Islands, Manus Island, *N. G. F. 543* (L, LAE).

PHILIPPINES. LUZON: Irosin, Mt. Bulusan, Prov. of Sorsogon, *Elmer 15595* (BM, F, G, GH, K, L, MO, UC, W); Pasacao, Camarines, *Ahern 40* (US). MINDANAO: Davao Prov., *For. Bur. 27538, De Mesa* (BM, L, NY, SING). PANAY: Prov. of Capiz, *For. Bur. 17832 Cortes & Rendal* (US). SAMAR: Mt. Cansayao, Catarman, in forest edge, *Phil. Nat. Herb. 14455, Sulit* (A, BM, L); Catubig River, *Bur. Sci. 24201, Ramos* (A, US); Loquilocon, Wright, *Bur. Sci. 43854, McGregor* (NY, UC), *Phil. Nat. Herb. 6055, Sulit* (A, L); without precise locality, *For. Bur. 12615, Rosenbluth* (NY, US).

1c. WRIGHTIA LAEVIS ssp. **NOVOGUINEENSIS** P.t. Ngan, ssp. nov. Affinis ssp. *millgar* a qua corona antheris paulo longiora et apice inaequaliter fimbriata differt.

NEW GUINEA: Bernhard camp, Idenburg River, in rain forest of mountain slopes, *Brass 13893* (A, BM, BRI, L, LAE); Kubuna, Central div., in rain forest of ridges, *Brass 5570* (A, HOLOTYPE, BM, BRI, K, NY, US).

Pichon was correct in recognizing the identity of *W. hainanensis* with *W. laevis*, yet he referred the latter to a variety of *W. tinctoria*. As I have pointed out in the section on species concept, these 2 species are quite distinct and easily recognized, for they differ not only in leaf characters but in the structure of the flower as well.

Although widely distributed from southern China to northern Australia *W. laevis* is a rather uniform population with the corona fimbriate, the alternating supplementary segments solitary and simple and the leaves glabrous to puberulent upon the veins beneath. In the western range the inflorescence is glabrous, while in the central and eastern ranges it becomes puberulent and the leaves more or less densely puberulent upon the veins beneath. Specimens collected in New Guinea have shown much variation in leaf and flower characters. However the material at hand is scant and many collections are sterile, and it is difficult to have an adequate appreciation of variation within this population. Therefore, in this study, I am referring it to subspecies *millgar* except ssp. *novoguineensis*, which is characterized by the unusually long and compound corona fimbriae.

Finally, *W. laevis* seems to hybridize with *W. viridiflora* occurring in Thailand. There are some specimens (*Kerr 15568, 17148*) which Pichon interpreted as *W. viridiflora;* however, I suspect that these are hybrids between the 2 species.

Although the few-flowered inflorescence and the stamens glabrous without combine to make these specimens apparently close to *W. viridiflora,* they are morphologically related to *W. laevis* on the basis of the leaves with 6 secondary veins, the relatively large flowers and the alternating corona segments as long as the antepetalous. Hence they are referred to *W. laevis* in this revision.

2. WRIGHTIA VIRIDIFLORA Kerr, Kew Bull. **1937:** 90. 1937. (T.: *Put 3086!*).

Shrubs or small trees as much as 5 m. high; branchlets rather slender, terete, glabrous to minutely puberulent, the bark gray to brown, striate. Leaves narrowly elliptic to elliptic, occasionally ovate to obovate, the apex acute to acuminate or mucronate, the base broadly acute, 8-15 cm. long, 2.5-7.0 cm. broad, membranaceous, glabrous above, puberulent to glabrous except upon the veins beneath, the secondary veins 9-12 pairs arcuate; petiole about 0.5 cm. long, puberulent. Inflorescence terminal, aggregate dichasial, few-flowered, much shorter than the subtending leaves; peduncle about 0.5 cm. long, the bracts small, scarious; pedicels rather slender, about 1 cm. long, glabrous to puberulent. Flowers relatively small, greenish, malodorous; calyx lobes ovate, acute about 1 mm. long, ciliate, minutely puberulent, bearing within 5 minute, alternate squamellae; corolla subrotate, the tube about 1.5 mm. long, glabrous, the lobes elliptic-obovate, acute, about 6 mm. long, minutely puberulent-papillate; corona fimbriate, as long as the stamens, glabrous, the antepetalous segments strongly adnate about half their length to the corolla lobes, about 3.5 mm. long, the alternipetalous deeply bifid, about 2.5 mm. long, the alternating supplementary segments simple, filiform, about 1 mm. long; stamens 5, inserted at the orifice of the corolla tube, the anthers glabrous without, puberulent within, the acumen glabrous, the filament relatively short, almost as long as the auriculate, basal anther lobes; carpels 2, free, glabrous, about 0.8 mm. long, the style slender, dilated near the tip. Follicles unknown.

Endemic to Thailand, in evergreen forests, on limestone; flowering from June to September.

THAILAND. AYUTHIA: Hin Lap, Saraburi, on rocky limestone hill, *Kerr 9128* (A, BM, K, L); Kao Sisiat, *Noe 105* (A, BM, SING); Menam Sak, Saraburi, on limestone rocks in evergreen forests, *Kerr 7061* (BM, E); Muak Lek, *Put 3086* (A, BM, E, K, L). RACHABURI: Brangkasi, about 100 km. south of Wangka, on rocky slope of limestone, *Den Hoed & Kostermans 678* (A, L); Bau re, Kanburi, *Put 196* (BM, K, MO); Kin Sayot, about 120 km. N. W. of Kanburi, on dry limestone rocks, *Kostermans 1093* (A, SING, US).

Wrightia viridiflora is closely related to *W. laevis* on the basis of the structure of the corona; however it differs from the latter in the few-flowered inflorescences much shorter than the subtending leaves, the relatively smaller, greenish and malodorous flowers and the alternipetalous corona segments shorter than the antepetalous. Pichon reported that this species also occurs in Vietnam, however I have seen no specimen from that area.

3. Wrightia flavido-rosea Trimen, Jour. Bot. **23**: 238. 1885. (T.: *Trimen s. n.* May 1884!).

Small trees, the branchlets slender, lenticellate. Leaves narrowly elliptic, the apex acuminate, the base acute, 10-15 cm. long, 2.5-3.5 cm. broad, membranaceous, sparsely and minutely puberulent on both surfaces, densely so upon the veins beneath, the midrib immersed above, prominent beneath, the secondary veins 10-13 pairs, arcuate towards the margins; petiole about 0.5 cm. long, puberulent. Inflorescence terminal, aggregate dichasial, rather lax, shorter than the subtending leaves; peduncle rather stout, about 0.5 cm. long, puberulent, the bracts minute, about 0.2 cm. long; pedicels about 1.3 cm. long, puberulent. Flowers yellow to pink-orange, becoming purplish-gray when withering; calyx lobes broadly ovate to very broadly ovate, acute, about 1.5 mm. long, puberulent without, bearing within 5 alternate, deltoid squamellae, about half as long as the lobes; corolla subrotate, the tube cylindrical, about 3 mm. long, the lobes narrowly obovate, obtuse, about 12 mm. long, minutely puberulent-papillate; corona of 3 series, fimbriate, a little shorter than the stamens, the antepetalous segments strongly adnate to the corolla lobes, relatively narrow, the alternipetalous bifid, the alternating supplementary segments solitary, simple, as long as the other two; stamens 5, inserted at the orifice of the corolla tube, about 7 mm. long, the anthers sparsely puberulent within, densely so without, the acumen barbate, the filament about 1.5 mm. long, glabrous, the basal anther lobes attenuate; carpels 2, densely pubescent at the tips, the style dilated near the subcapitate stigma. Follicles 2, coherent, about 22 cm. long; seeds about 1.8 cm. long, the yellowish coma about 4.5 cm. long.

Endemic to Ceylon, confined to the wet zone; flowering in May, fruiting in September.

Ceylon. northwestern province: Kurunegala distr., Doluwa Kande, May 1884, *Trimen s. n.* (K); same locality, September 1888, *Trimen s. n.* (UPS), *unknown collector s. n.* (UPS).

Although Pichon referred this species to *W. pubescens*, I believe that *W. flavido-rosea* is a distinctive species rather closely related to *W. laevis* on the basis of the corona structure. The relationships of this species with *W. laevis* have been discussed in connection with the chapter "Specific Concept." Furthermore, the unusually pubescent carpels also ally this species with *W. angustifolia*, occurring in the same area.

4. Wrightia **indica** P.t. Ngan, sp. nov.

Frutices vel arbusculae ramulis teretibus leviter puberulis. Foliorum lamina membranacea elliptica vel obovata apice acuminata vel acuta basi cuneata utrinque puberula costa superne impressa subtus prominente nervis secundariis 8-12 paribus; petiolus ca. 0.3 cm. longus minute puberulus. Inflorescentia terminalis aggregate dichasialis foliis aequalis; pedicellus ca. 0.8 cm. longus puberulusque; calycis laciniae ovatae obtusae ca. 2 mm. longae extus puberulae intus basi squa-

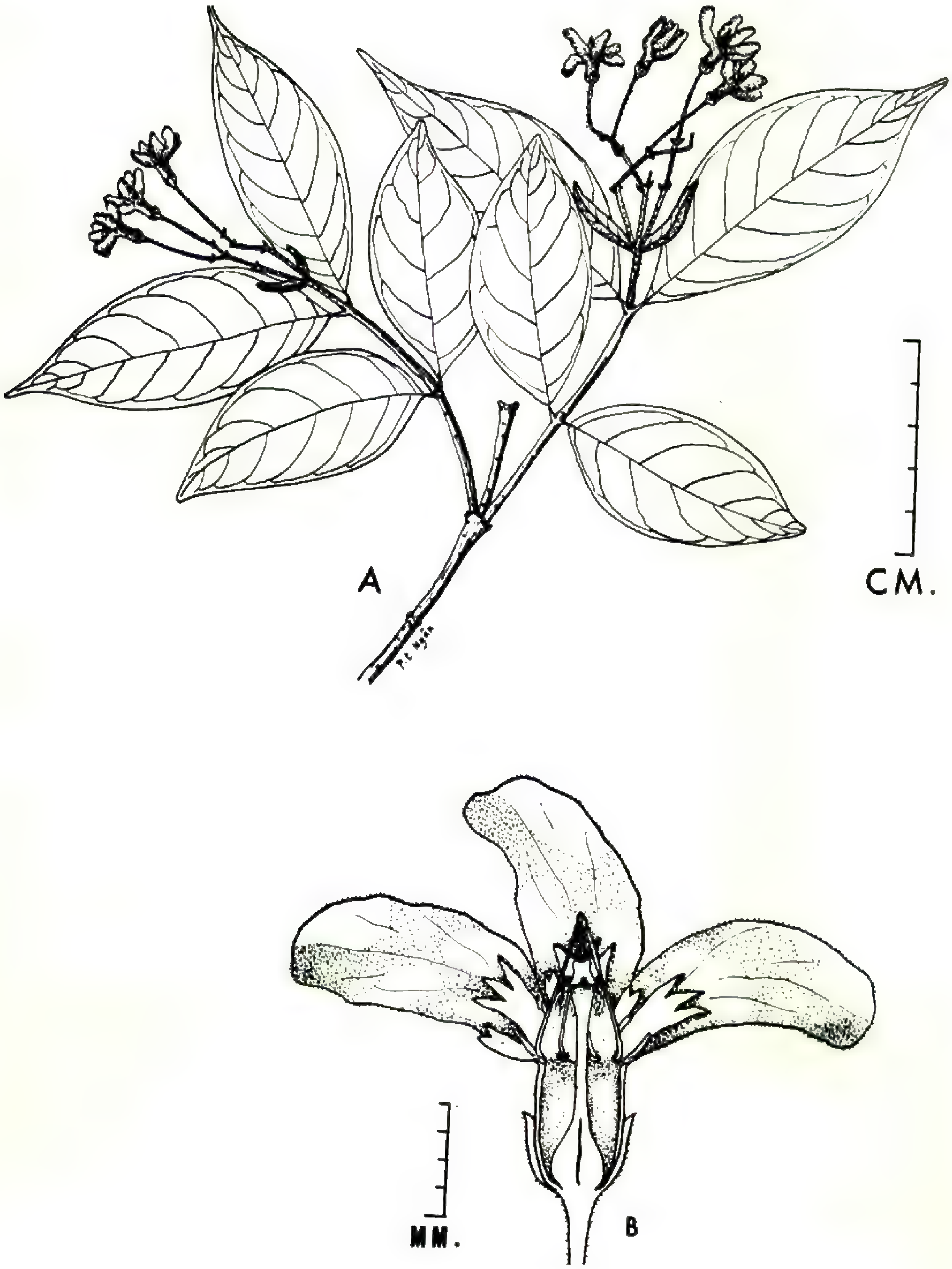


Figure 8. *Wrightia indica* P. t. Ngan; A, twig with inflorescences; B, longisection of the flower.

mellis deltoideo-ligulatis praeditae; corolla subrotata tubo subcylindrico ca. 4 mm longo lobis anguste subobovatis ca. 10 mm. longis puberulo-papillatis coronae squamis triseriatis glabris antepetalis tridentatis ca. 5 mm. longis alternipetalis brevioribus bifidis segmentis supplementalibus alternantibus solitariis simplicibusque; stamina ad faucem inserta antheris valde exsertis sagittatis ca. 6 mm. longis utrinque minute puberulis; carpella connata ca. 1.7 mm. longa glabra stylo ca. 5 mm. longo apice dilatato et stigmate subcapitato. Folliculi ignoti. Holotypus: *unknown collector 5117, Herb. Beddome* (BM).

Endemic to western and central Madras (India); up to 1000 m. elev.; flowering in June.

INDIA. MADRAS: Conoor ghat, *unknown collector 5117, Herb. Beddome* (BM); Hssur, Taluk, Salem distr., *Yeshoda 189* (NY).

This species has been confused in the herbarium with *W. tinctoria* ssp. *rothii* and *W. tomentosa,* from both of which it can be easily distinguished by the structure of the corona. *Wrightia indica* is rather a rare species characterized by the 3 series of corona segments with the alternating supplementary segments solitary and simple and the leaves puberulent throughout. It is closely related to *W. laevis* from which it differs in the antepetalous corona segments laciniate, the alternipetalous shorter and the carpels medially coherent.

5. WRIGHTIA TINCTORIA R. Br., Mem. Wern. Soc. **1**: 74. 1811. (T.: Roxburgh *s. n*!)

Small deciduous trees up to 6 m. high; branchlets terete, glabrous to densely puberulent, the bark smooth, striate, yellowish-gray. Leaves narrowly elliptic, occasionally broadly elliptic to narrowly obovate, acuminate to caudate-acuminate at the apex, acute to obtuse at the base, 6-24 cm. long, 2-9 cm. broad, membranaceous to chartaceous, glabrous to densely puberulent, the midrib immersed above, prominent beneath, the secondary veins 9-13 pairs, arcuate towards the apex; petiole very short, about 0.2 cm. long, glabrous to puberulent. Inflorescence terminal, aggregate dichasial, lax, divaricately branched, usually longer than the subtending leaves; peduncle rather slender, up to 1.5 cm. long, glabrous to puberulent, the bracts linear, about 0.5 cm. long; glabrous to pubescent; pedicels about 1.5 cm. long. Flowers white or lilac, fragrant; calyx lobes ovate to broadly ovate, about 2 mm. long, glabrous to puberulent, ciliate, bearing within 5 to many narrowly ovate squamellae, about as long as the lobes; corolla subrotate, the tube cylindrical, glabrous to puberulent at the orifice within, about 3 mm. long, the lobes narrowly obovate, obtuse, about 9 mm. long, puberulent-papillate; corona fimbriate, shorter than and up to as long as the stamens, the antepetalous segments strongly adnate to the corolla lobes, glabrous within to puberulent near the base, the fimbriae simple or compound, the alternipetalous bi- to multifid, about half the length of the antepetalous, the alternating supplementary segments geminate, much shorter than the antepetalous; stamens 5, inserted at the orifice of the corolla tube, about 7 mm.

long, the anthers puberulent throughout, occasionally glabrous without, the acumen barbate, the filament longer than the basal anther lobes; carpels 2, free, glabrous, the style slender, about 5 mm. long, slightly dilated near the subcapitate stigma. Follicles 2, free, sometimes coherent at the tips, slender and terete, 20-45 cm. long, lenticellate; seeds linear-fusiform, about 1.5 cm. long, the white coma about 4 cm. long.

Throughout India, in dry deciduous forests from approximately 25 to 1300 m. elev.; flowers from March to May, follicles in December-January.

KEY TO THE SUBSPECIES

a. Leaves narrowly elliptic or narrowly obovate to elliptic, glabrous, occasionally puberulent along the midrib beneath; inflorescence glabrous, occasionally puberulent upon the pedicels; antipetalous corona segments glabrous near the base within, the fimbriae usually simple. Plants of western, southern and eastern India. ....5a. W. TINCTORIA SSP. TINCTORIA

aa. Leaves elliptic to broadly elliptic, puberulent throughout; inflorescence puberulent; antipetalous corona segments puberulent near the base within, the fimbriae compound. Plants of northern and central India. ......5b. W. TINCTORIA SSP. ROTHII

5a. WRIGHTIA TINCTORIA ssp. TINCTORIA.

Nerium tinctorium Roxb., Hort. Beng. 19. 1818, nom. nud.; Fl. Ind., ed. Carey & Wall. **2**:4. 1824, ex char.

Wrightia laciniata A. DC. in DC., Prodr. **8**: 406. 1844. (T.: *unknown collector* s. n., photo. Mo!).

Wrightia timorensis Miq., Fl. Ind. Bat. **2**: 433. 1856. (T. : *Rijksherb. 2261/104*!).

INDIA. BIHAR: Hazaribagh distr. *Kerr s. n.* (BM). WEST BENGAL: Alipur, Calcutta, *Lancaster s. n.* (CAL); Ballygunge, Calcutta, *unknown collector 6* (CAL); Chandernagore, *Hosein 1* (CAL). BOMBAY: Birchy, north Kanara, *Talbot s. n.* (K); Borioli National Park, *Santapau 13061* (MO); Concan, *Lau & Stock s. n.* (BRI, CAL, G, GH, L, NY, W); Coorg, *unknown collector s. n.* (K); Karjat, north Concan, *Fernandes 251* (A); Khandala, *Santapau 4302* (CAL), *12918* (MO), *unknown collector s. n.* (E); southern Maratha country and north Canara, *Young s. n.* (CAL); Mercara, *unknown collector s. n.* (E, G, K, W); Salsette Island, *Perrottet s. n.* (G); Yellapur, Karwar distr., *Nana 5818* (CAL, K); without precise locality, *Cubbert s. n.* (L). MADRAS: Burliar, Nilgiris distr., *Gamble 11357* (CAL); Chingleput distr., *Gamble 10757* (K); northern Circar, *Campbell 40* (E); Coimbatore distr., *Fischer 1791* (CAL, K), *Rajagolsal Chetty 14* (EA); Dindigul, Pulney hills, Madura distr., *Anglade 647* (G), *914* (G); near Gingee Mt., *Delessert s. n.* (L); Guramkonda, Cuddapah distr., *Gamble 15045* (CAL, K); Jirugalli, Coimbatore, *Fischer 1072* (CAL); Jyamalai, near Coimbatore, *Brandis 1401* (A); Kadirinayanapalle, Nellore distr., *Ramaswami 1217* (CAL); Nilambur, *unknown collector 1031* (CAL); Nilgiri (Neilgherry), *Cleghorn s. n.* (E), *Lobb s. n.* (G, K), *Schmid s. n.* (CAL,) *unknown collector s. n.* (E); Pillearnatham, Madura distr., *Fischer 3135* (CAL); Pondichery, *Perrottet 93* (W), *321* (K), 322 (A, K, W), 325 (NY, US, W), *492* (G); Pulney hills, *unknown collector s. n.* (K, NY, UC); Pyapali, Kurnool distr., *Gamble 16493* (CAL); Salem distr., *Krishnan s. n.* (K); Taliparamba, Malabar distr., *Anstead 108* (A), *Barber 7728* (CAL); Tambracherighaut, *unknown collector 5693* (CAL); Tellicherry, *Vaid & Nautiyal 23336* (SING); Tuticorin, *Wright s. n.* (SING); Vizagatan, *Campbell s. n.* (E, G, UC). MYSORE: Maisor & Carnatic, *Thomson s. n.* (BM, CAL, F, G, GH, K, UPS, W); Shimoga, *Barber 7014* (CAL). RAJASTHAN: *Abu*, Barton *Grove s. n.* (CAL), *King s. n.* (CAL). TRAVANCORE-COCHIN: Puthanapuran, *Calder 1497* (CAL); without precise locality, *Rama Rao 2099* (CAL). INDIA: without precise locality, *Anglade 1819* (CAL), *Banks s. n.* (W), *Campbell s. n.* (G), *Courtallum 536* (E), 537 (NY), 538 (E), *s. n.* (BRI), *Hugel 1352* (W), *King s. n.* (CAL,) *Ritchie 1117* (E), *Roxburgh, s, n,* (E, G, K), *Russell s, n,* (W), *Wallich n. 1625 a* (G), *1625 B* (L, W), *Wright s. n.* (W).

5b. Wrightia tinctoria ssp. **rothii** (G. Don) P.t. Ngan, stat. nov.

Wrightia rothii G. Don, Gen. Syst. gard. bot. **4**: 86. 1838, ex char.
Wrightia tinctoria var. *rothii* (G. Don) Hook. f., Fl. Brit. Ind. **3**: 653. 1882.

India. ajmer: Ajmer, *Brandis s. n.* (CAL, K). bihar: Magadha, *unknown collector 728* (E); Monghyr hills near Jamalpur, *Kurz s. n.* (BM, CAL); Pokhuria, Manbhum, *Campbell 9284* (E); Rocky hills, Pathra forest, Gaya, *Haines 4272* (K). bombay: Badami, Bijapur distr., *Talbot 2773* (CAL). hyderabad: Manal, *Edwards 23* (K); without precise locality, *Campbell s. n.* (E, G). madhya bharat: Gwalior, *Maries s. n.* (CAL). madhya pradesh: Akola distr., *Watt 15* (E); Saugor, *Witt 24* (A); *Misra 51* (SING); Wamanpatti, south of Chanda, *Haines 2424* (K); exact locality unknown, *Hole 95* (CAL). madras: Adatigala, Yellavarani division, Godavari distr., *Ramaswami 1691* (CAL); Kadimakonda, Godavari distr., *Bourne 3571* (CAL, K); Kondapalli hill, Kistna distr., *Barber 8131* (CAL); Pyapalli, Kurnool distr., *Gamble 10974* (K), *Barber 8095* (CAL). orissa: Sonabear plateau, Sambalpur, on barren, very compact sandstone, *Mooney 3290* (K, NY); Montijharan hill, Sambalpur, frequent along the crest of sharp, quartz-schist ridges, *Mooney 3751* (A, K, NY). punjab: Karnal, *Drummond 25519* (E, G, UC); without precise locality, *Drummond 25517* (E G, K, UC), *25520* (E). rajasthan: Abu, *King 1115* (E); Abu, Sansevarra *unknown collector s. n.* (CAL); without precise locality, *Duthie 4736* (MICH). uttar pradesh: Banda, *Bell 310* (CAL); Delhi ridge, *Maheshwari s. n.* (G), *Stewart 7656* (A, NY); Manikpur, *Dudgeon & Kenoyer s. n.* (MO). vindhya pradesh: Chhatarpur, *Meebold 2964* (G). india: without precise locality, *Kabir 15184* (CAL), *King s. n.* (CAL), *Tamesion s. n.* (E), *unknown collector 2246* (E).

Wrightia tinctoria has been reported from Ceylon and as far east as Timor. Trimen (Jour. Bot. **23**: 238. 1885) pointed out that this species has not been found wild in Ceylon. As for Timor, I have seen specimens from this area identified as *W. tinctoria*, probably by Decaisne; they actually represent glabrous specimens of *W. pubescens* ssp. *pubescens*. Furthermore there is no difference between *W. tinctoria* ssp. *tinctoria* and *W. timorensis*, which was based on specimens referred to *W. antidysenterica* by Decaisne (Nouv. Ann. Mus. Hist. Nat. **3**: 379. 1834) and found in Timor to judge from the label. By virtue of the geographical disjunction I suspect an error in the locality data of these specimens.

Finally I interpret the 2 populations of *W. tinctoria* as allopatric subspecies because of the presence of intermediate specimens found at the commissure of their natural distributions. This suggests hybridization between the 2 subspecies.

6. Wrightia kwangtungensis Tsiang, *Sunyatsenia* **6**: 118. 1941. ex ic. & char. (T.: *Wang 23555*).

Shrubs up to 3 m. high; branchlets terete, gray to brownish, the bark striate and conspicuously lenticellate. Leaves elliptic to subobovate, acuminate to abruptly acuminate at the apex, acute at the base, 8-12 cm. long, 3.5-5.0 cm. broad, membranaceous, puberulent along the veins beneath, otherwise glabrescent, the midrib canaliculate above, prominent beneath, the secondary veins 8-10 pairs, arcuate; petiole 0.3-0.4 cm. long, minutely puberulent to glabrous. Inflorescence terminal, aggregate dichasial, half as long as the subtending leaves; peduncle about 0.8 cm. long, the bracts linear, about 1.5 cm. long; pedicels about 1 cm. long, puberulent. Flowers yellow, relatively large, about 2 cm. long; calyx lobes ovate, acute, about 2 mm. long, puberulent without, bearing within 5 broadly ovate, serrulate squa-

mellae about half as long as the lobes; corolla subrotate, the tube campanulate, relatively stout, about 4.5 mm. long, the lobes elliptic-obovate, about 15 mm. long, minutely puberulent-papillate; corona glabrous within, the antepetalous segments laciniate, strongly adnate to the corolla lobes, about 6 mm. long, the alternipetalous bifid, as long as the antepetalous, the alternating supplementary segments solitary and simple, about 3 mm. long; stamens 5, inserted at the orifice of the corolla tube, about 7 mm. long, the anthers densely puberulent, the acumen barbate, the filament definitely longer than the basal anther lobes; carpels 2, coherent, glabrous, the style gradually dilated near the subcapitate stigma. Follicles not seen.

Southern China and adjacent Vietnam, in shrubby savannas; flowering in May-June.

VIETNAM. Dachong, Sontay province, in savannas, *Pételot 5998* (A, NY).

Wrightia kwantungensis must be a rather rare species, to judge from the meagre herbarium representation. I have not seen the type but the description and illustrations of Tsiang match perfectly the specimen collected by Pételot in Vietnam. This species can be mistaken for the widespread *W. laevis* from which it differs in the size of the flowers, the laciniate corona segments and the coherent carpels.

7. WRIGHTIA **PUBERULA** (Thwaites) P.t. Ngan, stat. nov.

Wrightia rothii G. Don var. *puberula* Thwaites, Enum. Plant. Zeyl. 193. 1863. (T.: *C. P. 1837, Gardner s. n.!*).

Shrubs or small trees, the branchlets relatively slender, gray to pale brown, the current year's growth puberulent. Leaves narrowly elliptic to ovate, the apex acuminate to obtusely acute, the base cuneate, 8-12 cm. long, 2.5-3.5 cm. broad, membranaceous, sparsely puberulent on both surfaces, the midrid immersed above, prominent beneath, the secondary veins 10-12 pairs, arcuate towards the margins; petiole about 0.7 cm. long, puberulent. Inflorescence terminal, aggregate dichasial, relatively few-flowered, about half the length of the subtending leaves; peduncle rather slender, up to 1 cm. long, the bracts foliaceous, about 1 cm. long, very sparsely puberulent; pedicels about 1.5 cm. long, puberulent. Flowers moderately slender; calyx lobes ovate to broadly ovate, about 3.5 mm. long, minutely puberulent without, bearing within 5 ovate-deltoid squamellae shorter than the lobes; corolla subrotate, the tube cylindrical about 3.5 mm. long, the lobes narrowly oblong-elliptic, about 13 mm. long, puberulent-papillate; corona laciniate, a little shorter than the stamens, the antepetalous segments strongly adnate to the corolla lobes, the alternipetalous relatively broad, bifid to laciniate, as long as the antepetalous; stamens 5, inserted at the orifice of the corolla tube, the anthers very sparsely puberulent within, puberulent without, the acumen barbate, the filament glabrous, longer than the attenuate, basal anther lobes; carpels 2, free, glabrous, the style slender, dilated near the subcapitate stigma. Follicles not seen.

Endemic to Ceylon.

CEYLON. CENTRAL PROVINCE: Dambulla, *C.P. 1837 Gardner s. n.* (BM, G, K, W).

Thwaites, in describing Gardner's specimen, recognized it as a variety of *W. rothii* which, in turn, has been regarded as a variety of *W. tinctoria* by other authors who treated Gardner's collection the same. Although the 2 are superficially alike, *W. puberula* can be distinguished from *W. tinctoria* ssp. *rothii* on the basis of many reliable characters: absence of alternating supplementary segments, alternipetalous segments as long as the antepetalous, calycine squamellae ovate-deltoid, leaves sparsely puberulent throughout.

8. Wrightia sikkimensis Gamble, Kew Bull. **1908:** 447. 1908. (T.: *Gamble 574!*).

Wrightia schlechteri Léveillé, Repert. Sp. Nov. 11: 67. 1912 (T.: *Esquirol 111!*).
Wrightia stellata Pitard, Lecomte & Humbert, Fl. Gén. Indo-Chine **3:** 1186. 1933. (T.: *Bon s. n.*, photo. MO!).
Wrightia annamensis Eberh. & Duby, var. *coronata* Pitard in Lecomte & Humbert, *loc. cit.* 1192. 1933. (T.: *Eberhardt 1513*, photo. MO!).

Climbing shrubs or small trees, up to 10 m. high; branchlets slender, gray to brownish, the current year's growth glabrous to minutely puberulent. Leaves elliptic to oblong or ovate, occasionally obovate, the apex acute to long-acuminate, the base cuneate, 8-15 cm. long, 3-6 cm. broad, membranaceous to chartaceous, very minutely puberulent above, glabrous beneath except along the veins, occasionally glabrous or densely puberulent throughout, the secondary veins 9-12 pairs, oblique and curved towards the apex; petiole about 0.5 cm. long, minutely puberulent. Inflorescence terminal, aggregate dichasial, shorter than the subtending leaves; peduncle relatively long, 1.5-3.0 cm. long, minutely puberulent, the bracts linear-ovate; pedicels about 1 cm. long. Flowers dull yellow to red; calyx lobes ovate, about 2.5 mm. long, puberulent and ciliate, bearing within 5 alternate, ovate and serrulate squamellae; corolla subrotate, the tube about 2.5 mm. long, the lobes narrowly obovate, occasionally obovate, acute 12-14 mm. long, puberulent-papillate; corona glabrous within, the antepetalous segments subobovate, subentire, about 6 mm. long, the alternipetalous entire or bifid, about 2.5 mm. long; stamens 5, inserted at the orifice of the corolla tube, the anthers puberulent, the acumen barbate, the filament relatively slender, about 1 mm. long; carpels 2, free, glabrous, about 1.5 mm. long, the style slender, about 4 mm. long, gradually dilated near the subcapitate stigma. Follicles 2, free, terete-fusiform, 25-30 cm. long, conspicuously lenticellate; seeds linear, about 2 mm. long, the yellowish coma about 4 mm. long.

Northeastern India, southern China and northern Vietnam; at altitudes up to 1500 m.; flowers in April-May, follicles from June to September.

China. kwangsi: Bako Shan, west of Poshe, in woods, *Ching 7574*, (A, NY, UC, US); Ling Yun, in light woods, *Lau 28572* (A), *Steward & Cheo 515* (A, G, NY); Pan Shan, Ching Sai, in woods by hill, *Ko 55755* (A). kweichow: Bua Li, Cheng feng, in light woods, *Teng 91019* (A); La jong River, *Esquirol 111* (A, E); Lathong Wood, *Esquirol 3723* (E).

India. n. w. bengal: Darjeeling, Chunbati, *Gamble 574* (CAL, K), *3210* (CAL, K); below Kurseong, *Brandis s. n.* (K, NY); Panchkilla, *Clarke 26537* (US); Punkabari, *Clarke 35496B* (BM). east himalaya: exact locality unknown, *Biswas 3716* (A), *Modde 377K* (CAL). sikkim: without precise locality, *King 306* (CAL), *s. n.* (CAL), *unknown collector s. n.* (CAL).

The type specimen of *W. schlechteri* seems to have larger leaves, more or less chartaceous, the inflorescence relatively few-flowered and the flowers dull yellow. However these characters are within the range of the species and the floral structures of the 2 species are similar. Hence I am considering *W. schlechteri* as synonymous with *W. sikkimensis.*

I have not seen the type of *W. stellata* but the photograph and description show clearly its identity with *W. sikkimensis.* As for *W. annamensis* var. *coronata,* the stamens are obviously inserted at the orifice of the corolla tube and the detailed hand-notes on the photograph relate it to *W. sikkimensis.* Therefore I am tentatively including this variety under *W. sikkimensis.*

Wrightia sikkimensis appears to hybridize with other species growing within the same range. The puberulent leaves, the foliaceous bracts and the unusually large and dentate corona segments observed on specimens collected in India *(Biswas 3716, Modde 377K)* suggest possible hybridization with *W. tomentosa.*

9. WRIGHTIA TOMENTOSA (Roxb.) R. & S. Syst. Veg. ed. nov., **4**: 414. 1819, ex char.

Deciduous trees up to 20 m. high, without buttresses; branchlets gray to brownish, puberulent and lenticellate. Leaves elliptic to broadly elliptic or ovate, broadly ovate to obovate and broadly obovate, the apex acuminate to caudate-acuminate, the base acute, 7-18 cm. long, 3-8 cm. broad, membranaceous, densely puberulent beneath, puberulent to glabrescent above, the midrib immersed above, prominent beneath, the secondary veins 10-15 pairs, arcuate towards the apex; petiole 0.3-0.8 cm. long, densely puberulent. Inflorescence terminal, aggregate dichasial, few- to many-flowered, half to as long as the subtending leaves; peduncle 0.5-2.0 cm. long, puberulent, the bracts usually foliaceous, pubescent; pedicels 1.0-1.5 cm. long, puberulent. Flowers pale yellowish, pinkish or reddish, malodorous; calyx lobes ovate to broadly ovate, about 3 mm. long, puberulent, bearing within 5 ovate, serrulate squamellae, half to as long as the lobes; corolla subrotate, the tube 3-7 mm. long, glabrous, the lobes narrowly elliptic to obovate, 8-16 mm. long, puberulent-papillate; corona dull orange to purple, usually shorter than the stamens, glabrous within, the antepetalous segments crenulate to dentate, relatively broad, occasionally overlapping the alternipetalous, half their length adnate to the corolla lobes, the alternipetalous bifid, relatively broad, about as long as the antepetalous; stamens 5, inserted at the orifice of the corolla tube, the anthers sparsely puberulent to glabrous within, pubescent to minutely puberulent without, the acumen barbate, the filament relatively stout; carpels 2, coherent, about 1.5 mm. long, glabrous, the style columnar, gradually dilated near the subcapitate stigma. Follicles 2, coherent, broadly fusiform, stoutly apiculate, densely and conspicuously lenticellate, 17-35 cm. long; seeds linear-fusiform, about 1.5 cm. long, the white coma about 3.5 cm. long.

India, Ceylon, Burma, Thailand and adjacent China; in deciduous forests, mixed forests, thickets up to 1650 m. in altitude, along streams and on sandy or rocky soil; flowering from April to July, follicles from September to March.

Vernacular names: *Let-thoke* (Burma—Pokhant); *Atkura* (India—unknown collector); *Dudhi* (India—Kataky); *Chuang pa* (Thailand—Kasin); *Mok-man* (Thailand—Kokkamhaeng); *Muk Noi* (Thailand—Kerr).

KEY TO THE SUBSPECIES

a. Inflorescence many-flowered, lax; corona segments merely coherent at the base; corolla tube subcylindrical, more or less constricted at the orifice. Plants of India, Burma, Thailand and adjacent China. ....9a. W. TOMENTOSA SSP. TOMENTOSA

aa. Inflorescence few-flowered, condensed; corona segments coherent around the stamens; corolla tube campanulate. Plants of Ceylon. 9b. W. TOMENTOSA SSP. PAUCIFLORA

9a. WRIGHTIA TOMENTOSA ssp. TOMENTOSA

Nerium tomentosum Roxb., Hort. Beng. 6. 1814, nom. nud.; Fl. Ind., ed. Carey & Wall **2:** 6. 1824, ex char.
Hunteria eugeniaefolia Wall., Cat. n. 1615. 1828, fide Ind. Kew.
Wrightia coraia Wall., Cat. n. 1615. 1828, fide Ind. Kew.
Wrightia hamiltoniana Wall., Cat. n. 4461. 1828, fide Ind. Kew.
Wrightia mollissima Wall., Plant. Asiat. Rar. **2:** 39. 1831. (T.: *Wallich Cat. n. 1627!*).
Chonemorpha vestita G. Don, Gen. Syst. **4:** 76. 1836, fide Ind. Kew.
Nerium coraia Buch.-Ham. ex A. DC. in DC., Prodr. **8:** 407. 1844, ex char.
Wrightia tomentosa var. *roxburghii* A. DC., loc. cit. 405. 1844, ex char.
Wrightia wallichii A. DC. *loc. cit.* 1844. (T.: *Wallich Cat. n. 1628!*).

BURMA. Chin hill, *Shaik Mokim 456* (G); Hlegu forest, *Myanh s. n.* (EA); Insein distr., Myaukhlaing reserve, *Po Khant 248* (A); Kachin hills, *Shaik Mokim s. n.* (A, CAL); Keng Tung, *McGregor 719* (E); Mandalay, *Meebold 2988* (G); near Maymyo, *Fatteh Din 6202* (CAL, E), *Mg Kan 599* (CAL); Meiktila distr., in Taunggyigon reserve, *Tha Myaing 283* (E); Mindat, in thickets and forests on steep sunny slopes where forest is burnt, *Kingdon-Ward 22190* (BM), *22312* (BM); Myaungmya, *Dickason 6931* (A); Pegu, *Kurz 2367* (K); Rangoon, *Dickason 5668* (A); Shan hill, *Collett 801* (CAL, K); Takaw, *Kingdon-Ward 12762* (BM, E); Taunggyi, *Dickason 9320* (A); Tenasserim: Koung gee, *Gallatly 873* (CAL), Moulmein, *Falconer s. n.* (L), Pagaye, *Meebold 15013* (CAL), Taepo, *Gallatly 716* (CAL); Yamethin, *Rogers 566* (CAL, E). PRECISE LOCALITY UNKNOWN: *Shaik Mokim 76* (CAL, G), *828* (UPS).

CHINA. KWANGSI: Bako Shan, W. Poseh, in open woods, *Ching 7672* (W). KWEICHOW: Lohu, *Tsiang 7270* (NY), *7277* (W). YUNNAN: Che li hsien, Dah meng lung, in mixed woods, *Wang 77612* (A); Che li hsien, Sheau meng yeang, in woods, *Wang 75731* (A, UPS), *79618* (A); Chen kang hsien, along road side, *Wang 72139* (A); Fo Hai, in thickets, *Wang 74670* (A); between Muang Hai & Keng Hung, on bank of Nam Ha, *Rock 2483* (A, US).

INDIA. ANDAMAN: Middle Andaman, *Parkinson* 23 (K). ASSAM: Hathegain, *Chatterjee s. n.* (G, L); Silghat, Nowgong, *Prain s. n.* (A, CAL); without precise locality, *Herb. Hamilton 730* (E), *Jenkins s. n.* (E, L), *Simons s. n.* (CAL). BENGAL: Alipur, *Lancaster s. n.* (CAL); Darjeeling, *Clarke 26537C* (US), *Cowan s. n.* (E, US); Lalltung, *Biswas 6453* (A); N. Bengal, *Kurz s. n.* (CAL); Parganas distr., Gopikandar to Katikund, *Lace s. n.* (E); Siliguri, *Clarke 11675* (BM, CAL); precise locality unknown, *Kurz s. n.* (CAL). BHUTAN: Dang ma chu valley, *Cooper 4696* (BM); Kuruchu valley, *Cooper 4499* (BM); Singbhum, *Haines 672* (CAL, K). BIHAR: Baragaon, *Wood s. n.* (CAL, K); Chota Nagpur div., Palamau distr., *Gamble 8798* (CAL, K); Monghyr, *Lockwood s. n.* (K); without precise locality: *Hooker s. n.* (BM, CAL, G, GH, L, W). BOMBAY: Canara, *Ritchie 1118* (E); Concan, *Stocks, Law s. n.* (BM, BRI, CAL, E, G, GH, K, L, NY, UPS, W); Dharwar, *Dudgeon & Kenoyer 352* (MO, PH), *Sedgwick 3950* (A); North Thana div., *Gleadow s. n.* (E); S. Gujarat, Pimpri, *Bell 5455* (K); precise locality unknown, *Dalzell s. n.* (K), *Gibson s. n.* (E, NY), *Talbot 5* (CAL). HIMACHAL PRADESH: *Simor* distr., *Drummond 20633* (E, K). MADHYA PRADESH: *Chutia Nagpur, Campbell 9158* (E), *9221* (E); Melghat, *Witt 8026* (A). MADHYA BHARAT: Nimar distr., Punasu reserve, *Witt 1040* (A). MADRAS:

Coimbatore distr., Kallar, *Fischer 2059* (CAL); Godavari distr, Rampar, in dry deciduous forest, *Narayanaswami 622* (CAL); Kurnool, *Beddome 5122* (BM); Mamboli valley, Anaimalai hills, *Fischer 3359* (CAL); Nilgiris distr. Burliar, *Gamble 11359* (CAL, K); without precise locality, *Bourne 2738* (K), *2739* (K), *Jeffrey s. n.* (E), *Ramaswami 314* (CAL), *322* (CAL). MYSORE: Kumsi, Shimoga distr., *Meebold 8490* (CAL). NEPAL: Baglung, Kaligandaki River, on slope above river, *Stainton, Sykes & Williams 2745* (BM, E, UPS), *7006* (BM, E. UPS). PUNJAB: Dalhousie road, *Stewart 993* (NY, PH); Kangra distr., *Chowdri Ram 420* (E); Karnal, *Drummond 25604* (E, G, K, UC); Sutlej valley, *Cooper 5002* (E). ORISSA: near Labangi, Angul distr., *Lace 2567* (E). SIKKIM: without precise locality, *Hooker s. n.* (BRI, K, NY, W), *King 70* (CAL), *s. n.* (CAL). *Kurz s. n.* (CAL). SIKKIM HIMALAYA: Pankabari, *Cave s. n.* (E), *Clarke 26817* (CAL), *Gamble 3211 A* (K), *3212 A* (K), *3212 B* (CAL), *3213 A* (CAL), *Lister s. n.* (BM, CAL, NY). TRAVANCORE-COCHIN: Mundakhayam, *Bourdillon 201* (CAL). UTTAR PRADESH: The Bhabar, Kumaon, *Strachey & Winterbottom s. n.* (CAL, GH, K); Dehra Dun, *Forster 70* (CAL), *King s. n.* (CAL), *McKinnon s. n.* (CAL), *Raizada s. n.* (NY), *Sahai 97* (NY); Ghorawal Bhabar, *King s. n.* (CAL); Gonda distr., *Inayat 23713* (CAL); Kathgodam, *Meebold 2982* (G), *Poovaiah s. n.* (UC); Kumaon, *Hobart-Hampden 6* (E); Rajpur, near Dehra Dun, *Kataky s. n.* (NY); Saharanpur, *Gollan s. n.* (CAL); Singhighora Tarai, *Cave s. n.* (E); Terai, Gorakhpur distr. *Kurz s. n.* (CAL). PRECISE LOCALITY UNKNOWN: *Bell 6086* (CAL), *Brandis 1513* (CAL), *Clarke 43114B* (G), *Cleghorn s. n.* (CAL), *Cousins 2* (CAL), *Edgeworth s. n.* (K), *Gopal Nath 68* (UC), *Hugel 2847* (W), *Parish 1038* (K), *Parmeshwari Das s. n.* (W), *Roxburgh 254* (G), *s. n.* (E), *Russell s. n.* (W), *Stewart s. n.* (E), *Thomson 989* (BM), *1312* (BM), *Wallich Cat. n. 1626a* (G, PH), *1627* (W), *1627C* (BM, SING), *1628C* (L), *unknown collector s. n.* (E).

THAILAND. MAHARAT: Mae huad forest, Lampang, in mixed deciduous forest, *Kokkamhaeng 2514* (A, US); Me Tan, in mixed jungle, *Kerr 2564* (BM, E); Muang Pua, in deciduous jungle, *Kerr 5013* (BM, E, K). NAKAWN SAWAN: Meh Ping, Raheng, in deciduous jungle, *Winit 234* (BM, K). PAYAP: Chieng Mai, in dry mixed forest, *Kerr 5404* (BM); Meh Lee, Lampun, *Winit 235* (BM, K). RACHABURI: Brangkasi, about 100 km. S. of Wang Ka, in mixed forest along the river on sandy loam soil, *Kostermans 1462* (A, L); Hindato, 160 km. N. W. of Kanburi, in dry mixed forest on either gravel-like soil or rocks, *Kostermans 1362* (A); Wang Ka, on sandy soil, *Kasin 159* (A, BRI, G, L, SING); near Wang Ka, in secondary forest on low mountain ridge with much big bamboo, *Bloembergen 22* (A, BRI, G, K, L, SING).

9b. WRIGHTIA TOMENTOSA ssp. **pauciflora** P.t.Ngan, ssp. nov. A ssp. *tomentosa* inflorescentiis paucifloris et coronae squamis coherentibus differt.

CEYLON: WITHOUT PRECISE LOCALITY, *C. P. 2691* (BM, CAL, G, HOLOTYPE, W.); *Walker s. n.* (G, K).

Wrightia tomentosa is easily distinguished from the related species by the malodorous flowers, the corona shorter than the stamens, the antepetalous segments adnate about half their length to the corolla lobes and relatively broad, sometimes overlapping the alternipetalous. Some odd collections (type of *W. wallichii*) may have relatively short alternating supplementary corona segments and this feature has been shown clearly in Wight's illustration (Ic. Pl. Ind. Or. 4: pl. 1296 1850). At first I attempted without success to maintain these specimens as a distinct species upon other morphological characters. However, except for the feature mentioned above, these plants possess all of the attributes of *W. tomentosa* and since there is no geographical demarcation with the remainder of the population, I believe that they cannot be recognized even as subspecies.

Although *W. tomentosa* is relatively widely distributed from western India to Thailand and adjacent China, there is no appreciable variation in the morphological characters which might be correlated with the geographical distribution except the population in Ceylon that I am treating as a distinct subspecies. The

latter, with the few-flowered inflorescences and the coherent corona segments, might be set apart as a species when additional material is available for study.

10. Wrightia pubescens R. Br., Mem. Wern. Soc. **1:** 73. 1811. (T.: *Brown 2861*, photo. MO!).

Trees up to 35 m. high, the trunk columnar, without buttresses; branchlets terete, gray to dark brown, glabrous to densely puberulent when immature. Leaves narrowly ovate, ovate to elliptic or oblong-ovate, occasionally obovate, the apex acuminate to abruptly caudate-acuminate, the base acute to obtuse, 5-15 cm. long, 2.0-6.5 cm. broad, membranaceous to subchartaceous, glabrous except upon the veins beneath to densely puberulent or glabrescent above, the midrib canaliculate above, prominent beneath, the secondary veins 8-15 pairs, arcuate toward the apex; petiole 0.4-0.8 cm. long, puberulent. Inflorescence terminal, aggregate dichasial, many-flowered, rarely few-flowered, half to as long as the subtending leaves; peduncle 0.5-1.5 cm. long, puberulent, the bracts tiny and scarious to relatively large and foliaceous; pedicels about 1 cm. long, puberulent. Flowers white, cream, yellow to pink, orange or dark red, fragrant; calyx lobes broadly ovate to ovate, acute to obtuse, 2-5 mm. long, glabrous to densely puberulent without, bearing within 5 ovate, acute to serrulate squamellae about half up to as long as the lobes; corolla subrotate, very rarely infundibuliform, the tube subcylindrical to campanulate but usually constricted at the orifice, sometimes provided with a callous faucal annulus, 5.0-6.5 mm. long, the lobes narrowly obovate to obovate, acute to obtuse, 10-20 mm. long, puberulent-papillate; corona usually about as long as the stamens, glabrous to puberulent within, the segments free from each other or coherent at the base, the antepetalous dentate, crenulate, bifid or subentire, relatively broad, usually medially adnate to the corolla lobe, the alternipetalous much shorter to almost as long as the antepetalous, subentire to bifid; stamens 5, inserted at the orifice of the corolla tube, very rarely below, the anthers exerted, very rarely included, puberulent, the acumen barbate, the filament relatively broad, longer than the basal anther lobes; carpels 2, coherent, glabrous, the style gradually dilated near the subcapitate stigma. Follicles 2, coherent, 15-30 cm. long, finely striate, obscurely to conspicuously lenticellate; seeds linear-fusiform, yellowish to gray, about 1 cm. long, the white coma about 3.5 cm. long.

Widely distributed from southern China to northeastern Australia through Ceylon, Thailand, Indochina, Indonesia, and Philippines and the Solomon Islands; in evergreen and deciduous forests and thickets; flowering mostly from April to September, fruiting from August to February.

Vernacular names: *Cherite* (Australia—Bailey); *Foo yung shue* (China—Lei); *To tiu Pat* (China—McClure); *Ue tsueng shue* (China—Tsang); *Yu chang* (China—Lau); *Muntow* (Malay—Curtis); *Anaotung* (Philippines—Balintay); *Lanete* (Philippines—Lambert & Brunson); *Manlagosi* (Philippines—Zaldua); *Mok* (Thailand—Kerr); *la moc* (Vietnam—Pierre).

Fig. 9. *Wrightia pubescens* R. Br. ssp. *laniti* (Blco.) P. t. Ngan; A, twig with inflorescences; B, longisection of the flower.

KEY TO THE SUBSPECIES

a. Calyx ⅔ to as long as the corolla tube, the lobes acute to obtuse, 3.5-5.5 mm. long.
  b. Antepetalous corona segments dentate, puberulent to glabrous within; calyx about the length of the corolla tube. Plants of Indonesia, New Guinea and northwestern Australia. ....10a. W. pubescens ssp. pubescens
  bb. Antepetalous corona segments subentire, crenulate, rarely dentate, glabrous within; calyx ⅔ to as long as the corolla tube. Plants of the Philippines. ....10b. W. pubescens ssp. candollei
aa. Calyx ¼ to half as long as the corolla tube, the lobes acute, about 2.5 mm. long.
  c. Corona segments subentire, the alternipetalous much shorter than the antepetalous, sometimes inconspicuous. Plants of New Britain. ....10c. W. pubescens ssp. novobritannica
  cc. Corona segments dentate to crenulate, the alternipetalous ⅔ to about as long as the antepetalous.
    d. Corona glabrous within; leaves glabrous, occasionally puberulent. Plants of northeastern Australia ....10d. W. pubescens ssp. penicillata
    dd. Corona puberulent within; leaves densely puberulent to glabrescent above. Plants of Burma, Ceylon, China, Thailand, Indochina, Malaya, The Philippines and western Java. ....10e. W. pubescens ssp. laniti

10a. Wrightia pubescens ssp. pubescens

Nerium macrocarpum Span., Linnaea **15:** 325. 1841, nom. nud.
Nerium jaspideum Span., *loc. cit.* 1841, nom. nud.
Nerium multiflora Zipp. ex Span., *loc. cit.* 1841, nom. nud.
Wrightia spanogheana Miq., Fl. Ind. Bat. **2:** 434. 1856. (T.: *Spanoghe s. n.*!).
Wrightia calycina A. DC. in DC., Prodr. **8:** 406. 1834. (T.: *unknown collector* in *Herb. Mus. Paris 1876*!).

Australia. northern territory: Bradshaw Creek, *Blake 17295,* Daly River, *Blake 16631* (BRI), *Campbell s. n.* (NSW); Darwin, in monsoon forest on top of sea cliff, *Blake 17327* (BRI); East Point, Darwin, *McKee 8295* (CANB, NSW); Nightcliff, Darwin, in monsoon forest on truncated lateric podsol, *Chippendale 7872* (CANB, NSW), *Spetch 156* (BRI, CANB); Port Darwin, *Holtze 347* (MEL), *629* (MEL); Port Essington, *Armstrong s. n.* (NSW); North of lake Finniss, in monsoon forest on grey lateric soil, *Blake 17015* (BRI); Fitzmaurice River, *Mueller s. n.* (MEL); Oenpelli, at foot of sandstone hill, *Spetch 1168* (CANB, L, MEL, NSW, US); without precise locality, *Holtze 1198* (BRI, MEL).

Indonesia. alor: G. Kojakojo, Kampong Naumang, *Jaag 1084* (BM, L.). bali: Prapat Agung, *Becking 45* (L), *Kostermans, Kuswata, Soegeng & Soepadmo 10* (L). celebes: Bikeru Balang, *Warburg 16325* (A); Kandari, *F. R. I. bb. 24979* (L); Lapankanrae, *Noerkas 251* (L); Manado, *F. R. I.*, bb. *15045* (L); Moena, Wasalangka, *F. R. I. bb. 21611* (A, L); Saleier, *Teysmann 13602* (L), *F. R. I. bb. 24109* (L.). java: east java: Bangil, *Backer 7571* (L); Banjuwangi, *Koorders 38905β* (L); Bondowoso, *Backer 9529* (L), *F. R. I. Ja. 2811* (A, L); Kediri, *Coert 152* (L); Madura Island, near Sumenep, *Zollinger 3824* (W); Probolinggo —G. Tengger (Bromo), *Kuntze 5959* (NY); Puger, *Koorders 199β* (L); Surabaja, *Backer 26577* (L); without precise locality, *de Vriese & Teijsmann s. n.* (L), *Zollinger 1228* (W). central java: Surakarta, *Horsfield s. n.* (BM, GH, K). leti islands: Moa, Lakor, *Riedel s. n.* (K). lombok: Sadjang, *Elbert 742* (L). N. moluccas: Tidore, *de Vriese s. n.* (L). sumba: 7 km. from Waingapu, *Jaag 21a* (L). sumbawa: Bima, *Elbert 3650* (L), *3898* (L, SING), *Warburg 17189* (E). tanimbar islands (timor laut): Jamdena, Saumlaki, in abandoned field, *Borssum W3122* (L); Jamdena, Olilit near Saumlaki, on open grounds, *Pleyte 27* (L); without precise locality, *Meyer s. n.* (K), *Pereira, s. n.* (SING). timor: Baucau, *Van Steenis 18029* (BM, CANB, L); Nipol, *Walsh-Held 230* (BM); Obe Naih, in savanna, *Bloembergen 3346* (L); without precise locality, *Spanoghe s. n.* (L), *Zippelius s. n.* (L), *unknown collector* in Herb. *Mus. Paris 1876* (K), *unknown collector 61* (L), *s. n.* (G, L,

NY). WETAB: Tara, in Eucalyptus forest, *Bloembergen, 3743* (CANB, L). WEST IRIAN (WEST NEW GUINEA): *Merauke, Branderhorst 284* (K, L), *Versteeg 1912* (L); Okaba, *Branderhorst 144* (L).

10b. WRIGHTIA PUBESCENS ssp. **candollei** (Vidal) P.t.Ngan, stat. nov.

Wrightia candollei Vidal, Phan. Cuming. Philipp. 186. 1885. (T.: *Cuming 1453*!).

PHILIPPINES. BILIRAN: without precise locality, *Bur. Sci. 18579, McGregor* (A, BM, US). BOHOL: Bihar, thicket forest, *Bur. Sci. 42712, Ramos* (A, UC, US). CAMOTES ISLANDS: *Bur. Sci. 41607, Ramos* (A, L, US). CEBU: *For. Bur. 27331, Lopez & Reyes* (A, BM, L). GUIMARAS ISLANDS: *For. Bur. 228, Gammill* (K, US). LUZON: Albay Prov., *Cuming 1293* (BM, K, W). Bataan Prov., Olongapo Naval reservation *Bartlett 14074* (A, MICH). Batangas Prov., Mt. Lobo Bo, in secondary growth forest, *Phil. Nat. Herb. 7428, Sulit* (A). Bulacan Prov., vicinity of Kay Tianak & Ipo, *Bartlett 14720* (A). Mountain Prov., Bengued, Twin Peaks, *Elmer 6348* (K, NY, US); Castilla, La Union, *Loher 6542* (K, US). Nueva Ecija Prov., *For. Bur. 8442, Curran* (MO). Pangasinan Prov., Bolinao, on coral rocks, in thickets by sea, *Clemens 18171* (SING, UC, W), *Bur. Sci. 8284, Ramos* (L). Rizal Prov., Manila, *Gallery s. n.* (G), *Vidal 1009* (A), *3275* (A, K); Morong, Bosoboso, *Merrill 2791* (BM, K, NY, US), *Vidal 3274bis* (K); Montalban, *Loher 3994* (K), *6519* (K), *6530* (K), *s. n.* (UC); San Mateo, *Ahern 1116* (BM, K, NY, US); without precise locality, *For. Bur. 3155*, Ahern (F, K, NY, SING, US), *Cuming 1453* (BM, G, K, UPS, W), *Bur. Sci. 6757, Robinson* (BRI, L). MASBATE ISLAND: *Merrill 3049* (BM, K, NY, US), *3082* (BM, K, L, US). MINDANAO: Lanao Lake, Camp Keithley, *Clemens 1060* (F). MINDORO: Mabaho ridge, Kabalwa, *Phil. Nat. Herb. 17044, Sulit* (A, BM); without precise locality, *Bur. Sci. 21296, Escritor* (BM, K, US). NEGROS: *Bur. Sci. 23404, Contreras* (A, US). PALAWAN: Apulit Island, Taytay Bay, Merrill 9426 (BM, BRI, F, GH, L, HO, NY, SING) (US); Puerto Princesa, *For. Bur. 19906, Danao* (US); without precise locality, *For. Bur. 4510, Curran* (K, L, US), *Bur. Sci. 1183, Fenix* (BM, G, US). TICAO ISLAND: *Vidal 3276* (A, K). WITHOUT PRECISE LOCALITY: *Cuming s. n.* (BM).

10c. WRIGHTIA PUBESCENS ssp. **novobritannica** P.t.Ngan, ssp. nov. Affinis ssp. *calycinae* sed calycis laciniis brevioribus et foliis anguste oblongo-ellipticis differt.

NEW BRITAIN. Nodup area, *Waterhouse 270* (A, F, NY, HOLOTYPE, US).

10d. WRIGHTIA PUBESCENS ssp. **penicillata** (Bailey) P.t. Ngan, stat. nov.

Wrightia pubescens var. *penicillata Bailey Queensl.* Fl. **6:** 2010. 1902. (T.: *Bailey 389*!).
Wrightia versicolor S. T. Blake, Proc. Roy. Soc. Queensl. **59:** 163. 1948. (T.: *Blake 14702*!).

AUSTRALIA. QUEENSLAND: Cook distr.: Fitzroy Island, *unknown collector 29* (MEL); Lizard Island, *Walter s. n.* (MEL); *Mapoon, Bailey 389* (BRI), *s. n.* (BRI); Mount Surprise Creek, *Armit 766* (MEL); 100 miles Swamp, in scrub, *Armit 807* (MEL). *North Kennedy distr.:* 13 miles N. of Charter Towers, in rather open monsoon forest on hard reddish sandy soil, *Blake 14672* (BRI); Barrabas Scrub, W. Ravenwood, in monsoon forest on deep loose coarse whitish sand, *Blake 14702* (BRI), *14893* (BRI).

10e. WRIGHTIA PUBESCENS ssp. **Laniti** (Blco.) P.t. Ngan, stat. nov.

Anasser laniti Blanco, Fl. Filipp. 112. 1837, ex char.
Wrightia ovata A. DC. in DC., Prodr. **8:** 405. 1844. (T.: *Cuming 1279, 1802*!).
Wrightia javanica A. D.C. in DC., *loc. cit.* 1844. (T.: *Kollman s. n.*!)
Wrightia laniti (Blco.) Merrill, Gov. Lab. Publ. **27:** 59. 1905.
Wrightia tomentosa var. *cochinchinensis* Pierre ex Pitard, Lecomte & Humbert, Fl. Gen. Indo-chine **3:** 1186. 1933. (T.: *Pierre 1047*!).

Cambodia. Pnompenh, *d'Alleizette s. n* (L); without precise locality, *Bejeaud 261* (A, NY, SAIG).

China. hainan: Chim fung Ling, in thicket on dry, gentle slope, sandy soil, *Lau 3890* (A); Chung kon, *Gressitt 1028* (A, BM, E, G, MO); Fingan, *Katsumata s. n.* (BM); Hoi how, *Bullock s. n.* (BM), *Hancock 38* (K), *Tsang, Tang & Fung 4* (A); Hui ka, Lin Fa Shan, Lam ko distr., *Tsang 203* (A, G, K, NY, UC, US); Lam ko distr. & vicinity, *Lei 1438* (A); Hung mo shan, Lai area, *Tsang & Fung 698* (A, K, NY, US); foot of Hung shek Lang, *Tsang 71* (A, G, MO, UC, US); Ka chik Shan, fairly common in thicket, *Lau 1666* (A, BM, NY); I Kap Shan, Tan Distr., *Lau 1169* (BM, NY); Keuk Ha Tsun, *McClure 8911* (A, BM, E, F, G, K, MO, UC); Kieng chau fu, *Henry 7956* (E, K), *13724* (BM); *Kiung* chau, *Fung 20314* (A, BM, HK, K, NY, UC, US, W); Lar tai shee, *collector unknown 392* (A, K); Nam shan Leng, Ngai distr., in swamp, sea shore, on sandy soil, *Lau 314* (A, BM, E, G, K, MICH, MO, NY, UC, US, W); Nodoa, *McClure 9820* (US); road to Onzin, *Chun 994* (UC); Paai Poon Tsuen, on sea shore, *Fung 20250* (A, BM, E, G, K, NY, UC, US); Pak shik Ling, Ching mai distr., *Lei 608* (K, NY, US); Poting, in forest, *How 71954* (A, SING); east Poting, Lingshui, *Ko 52217* (A, NY); Tai Por, foot of Seven Finger Mt., *Liang 61690* (A, K, NY, US); Tai wong Ling, *Lei 209* (HK, K, NY, SING, UC, US, W); Tai wong Shan, *unknown collector 2181* (HK); Ue Lung Shan, Chang kiang distr., *Lau 3188* (A); Yai chau, in forest, *Chun & Tso 44515* (A, E, NY), *How 70752* (A, L, NY), *How & Chun 70218* (A, K, NY, US), *Liang 62396* (NY), *63003* (NY); without precise locality, *Henry 8289* (K), *8751* (GH), *Katsumada s. n.* (UC), *Liang 63660* (NY), *64616* (NY), *66178* (E, G, NY), *Wang 33381* (A, NY, US), *35103* (NY, US), *36202* (A, NY), *Wu 1109* (BM). kwangtung: Canton, *Ford 264* (HK, K, NY), *Levine 221* (A, F, HK, MO, US), *2128* (A, GH, HK, MO), *Merrill 10110* (A, HK, UC); Honam, *Hoffman 72* (NY); Honan, Chik Cha village, on road side, *McClure 1707* (E, G, W); Honan, near Ha to, in bushes, *McClure 1703* (K, UC); Honan, east of Taai Tong, *McClure 1671* (A, BM, K, UC, US), *1672* (E, G); Hop Po city, *Liang 69302* (A); Kochow, *Tsiang 886* (A), *2786* (A); Pei Yun Shan, *Tsiang 450* (A, E, UC); Po tan, Luichow, Hoi kong distr., *Tsiang 2534* (A, BM, NY); Quenyinshan, *Tsiang 406* (BM, E, K, NY, SING); San Ning, *Wong Ke s. n.* (HK); White Cloud Mt., *Levine 2044* (A, HK, MO); Vutzeling, Kochow, in dense scrubs, *Tsiang 2308* (NY); without precise locality, *Ford 335* (K), *Haunton s. n.* (BM), *McClure 13495* (UC). kwangsi: without precise locality, *Liang 70102* (A).

Indonesia. java: Bantam: Tjimara, *Koorders 196β* (L); Batavia: *Backer s. n.* (L), *Bakhuizen v. d. Brink 4892* (L); Cheribon: Kalidjohopekik, *Koorders 36598β* (L); Krawang: Poerwakarta, *Koorders 13798* (L), *13799* (CAL, K, L), *14232* (K); Pekalongan: Soebah, *Koorders 13800* (CAL), *13800β* (K), *13801β* (L), *13802* (CAL, K, L), *13802β* (L), *14229* (L), *14232β* (CAL), *14244β* (K, L,), *22549β* (L), *27294β* (L); Preanger: *Palabuanratu, Koorders 194β* (L), *200β* (L, UC); Soekaboemi, *Koorders 12232β* (L); Tomo, Koorders *195β* (L); Semarang: Geboegan, *Koorders 198β* (A, L); Karangasem, *Koorders 38874β* (L); Solo, Kedoengdjati, *Koorders 33704β* (L); without precise locality, *Backer & Coert 804* (L), *Zollinger 598* (A, BM, G, L). sumatra: without precise locality, *unknown collector 230* (L).

Malaya. kedah: Alor Star, *Ridley 14950* (K, SING), *14951* (BM, K, SING); Jitra, *Burkill S.F.N. 13349* (SING); Tasch Gelugor, *Curtis 3738* (CAL, K, SING); without precise locality, *Kunstler 1762* (CAL). perak: Lake Gardens, Taiping, *Corner s. n.* (SING). perlis: *Ridley 14952* (BM, SING). trengganu: Kuala Trengganu, *Sinclair S.F.N. 39986* (BM, E, L, SING).

Philippines. culion: Calamaian Island, in dry open valley, *Merrill 676* (BM, GM, K, MO, NY, SING, US); without precise locality, *Herre 1049* (A, NY, UC, US). cuyo: *Bur. Sci. 15540, Kienholz* (UC). luzon: Bataan Prov., Dinalupihan, *Merrill 1486* (K, US); Lamao River, Mt. Mariveles, *For. Bur. 770, Borden* (F, NY, SING, US), *For. Bur. 3067, Borden* (F, NY, US) *Whiteford 1260* (NY, US); without precise locality, *For. Bur. 23206, Alambra & Caulas* (A, SING), *For. Bur. 12939, Alvarez* (L), *For. Bur. 22701, Gangan* (A), *For. Bur. 25694, Miras* (UC), *For. Bur. 23062, Pascual* (L), *For. Bur. 27780, Ranario* (SING), *For. Bur. 25679, Sulit* (K), *For. Bur. 20009, Topacio* (BM). Batangas Prov., Mt. Lobo, *Phil. Nat. Herb. 15715, Sulit* (A); Taal Volcano, *Gates 8373* (MICH), *Gates & Quisumbing 7951* (MICH). Bauco Prov., Bontoc, *Vanoverbergh 3117* (US). Bulacan Prov., *For. Bur. 24730, Leuterio* (BM, L). Cagayan Prov., Enrile, *Clemens 17541* (BM, W); vicinity of Peñablanca, *Adduru 197* (A, F, MO, US); without precise locality, *For. Bur. 15138, Bernardo* (L), *Bur. Sci. 22746, Castillo* (HK, US), *Cuming 1279* (BM, G, K, L, MO,

NY, UPS, W). Cavite Prov., *Bur. Sci. 22555, Ramos & Deroy* (GH, MO, SING, US). Ilocos norte Prov., *For. Bur. 22999, Adduru* (A, BM). Isabella Prov., San Mariano, *Bur. Sci. 46675, Ramos & Edano* (UC), *Bur. Sci. 47008, Ramos & Edano* (UC), *For. Bur. 30396, Siriban* (NY, SING, UC); without precise locality, *For. Bur. 26288, Barros* (GH). Laguna Prov., Los Banos, *Elmer 8069* (E); Makiling National Park, *Phil. Nat. Herb. 6875, Sulit* (A), *Phil. Nat. Herb. 22879, Sulit* (BM, US); Mt. Makiling, *For. Bur. 19784 Whitford* (BM, K, L). Nueva eciza Prov., *For. Bur. 24142, Tungol* (A, F, GH, MO). Nueva vizcaya Prov., vicinity of Dupax, *Bur. Sci. 11298, McGregor* (G, MO), *Bur. Sci. 11300, McGregor* (BM, K, L, US); without precise locality, *McGregor 4630* (L). Pangasinan Prov., *For. Bur. 24577, Mayor* (BRI). Rizal Prov., Antipolo, *Ahern 90* (A, US), *Guerrero 31* (US); Manila, *Garcia s. n.* (W), *Loher 3999* (US), *Perrottet s. n.* (G); Morong, Bosoboso, *Loher 4000* (K, US), *Merrill 1848* (K, US), *2833* (K, NY, US), *Bur. Sci. 1462, Ramos* (NY, US); without precise locality, *For. Bur. 2960, Ahern* (F, NY, SING, US), *For. Bur. 3336, Ahern* (MO, US), *For. Bur. 17856, Franco* (GH, US), *For. Bur. 27160, Mariano* (F, MO), *Merrill, species Blancoanae 562* (A, BM, F, GH, K, L, MO, NY, US, W), *Ramos 26* (G, US), *Bur. Sci. 2042 Ramos* (BM, BRI, G, GH, L, MO), *Bur. Sci. 6738, Robinson* (BRI). Zambales Prov., Mt. Pinatubo-Villar, in Grassland, *Balintay 555* (A); Subic, *Merrill 1753* (K, US), *1978* (US), *2112* (K, NY, US). MINDANAO: Cotabato Prov., Buayan, in secondary forest, *Bur. Sci. 85136, Ramos & Edaño* (A). Zamboanga Prov., *Ahern s. n.* (US), *For. Bur. 24590, Franco* (BM), *Bur. Sci. 37465, Ramos & Edaño* (A). MINDORO: Ilin Island, *For. Bur. 29850, Zaldua* (NY, UC), *For. Bur. 29852, Zaldua* (UC); Paluan, *Bur. Sci. 39677, Ramos* (A); Pandarucan, *Merrill 943* (GH, K, NY, US); Puerto Galera and vicinity, on hill near the shore, *Santos 5259* (US); vicinity of San José, *Lambert & Brunson 130* (US); east of Yagaw, *Conklin 1030* (L, US); precise locality unknown, *For. Bur. 9801, Merritt* (MO), *Vidal 3273bis* (K). NEGROS: Negros oriental Prov., Dumaguete, Mts. Cuernos, in dry thickets along the Ocoy River, *Elmer 10291* (A, BM, E, F, G, L, MO, NY, US, W); without precise locality, *Cuming 1802* (BM, K, W). PALAWAN: Taytay, *Merrill 9200* (A, BM, F, GH, L, MO, NY, US); without precise locality, *For. Bur. 29949, Cenabre* (UC).

THAILAND. CHANTABURI: Chantabun, *Verterdal 9L* (SING). KRUNGTEP: Bangkok, *Kerr 10702* (BM, E, L), *Marcan 2085* (BM). NAKAWN SAWAN: Sriracha, in thickets along the beach, *Collins 10* (K), *Kerr 4260* (BM); without precise locality, in mixed forest, *Kerr 5977* (BM). NAKAWN SRITAMARAT: Saba Yoi, Songkla, *Kerr 14789* (A, BM, E, K, L). PUKET: Betong, Satul, on rocky ground, *Kerr 14062* (BM, E, K, L); Tongkah, *Curtis 3054* (CAL, SING). RACHABURI: Hua Hin, *Kerr 16199* (BM), Baw Fai, *Marcan 2482* (BM); Prachuap, *Put 261* (BM, E, K, L); Sam Roi Yawt, Prachuap, in evergreen forest, *Kerr 10899* (BM, E, L); Wang Yai, Kanburi, in deciduous forests, *Charoenmayu 405* (US), in scrub jungle, *Kerr 10110* (BM, K). SURAT: Kaw Samui, *Put 863* (BM, E, K, L, SING); Kaw Tao, in dry evergreen forest, *Kerr 11117* (A, BM, K), in open evergreen forest, *Kerr 12685* (A, BM, K). WITHOUT PRECISE LOCALITY: *Marcan 1686* (BM).

VIETNAM. Biênroa, *Chevalier 35562* (SAIG), *Pierre 1147* (A, SAIG); Choganh. *Du Pasquier 958* (UC), *995* (A, NY, UC, US), *1267* (UC); *Côndao* (Poulo Condor), *Harmand 694* (A); Hānôi, *d'Alleizette s. n.* (L), *Fleury 37728* (L); Hōabīnh, *Pételot 6991* (A, NY), *Poilane 13006* (SAIG); Langson, Dongmo, in open forest, *Pételot 2436* (A, MO); Phu hô, *Du Pasquier 1875* (UC), *1926* (UC); Nha trang, *Chevalier 39495* (SAIG); *Phutuson, d'Alleizette s. n.* (L); *Phúcyén Pételot 5944* (A, NY, US); Quang tri, *Poilane 13323* (SAIG); Sāigōn, *Pierre 1047* (A, K, L, MO, NY, SAIG, SING) *Thorel 696* (A, F, K, NY, UC); Sonla, *Colani 4038* (UC); Sontây, *Pételot 2446* (A, MO), *6003* (A); Tháinguyên, *Pételot 6988* (A, NY); Tupháp, *Balansa 2120* (G, L, NY, SAIG), *2121* (K); Vinh and Baubō, *Spire 570* (SING). Without precise locality, *Balansa s. n.* (G), *Dong phuc Long 1303* (SAIG).

The several synonyms here are due to the wide distribution and the morphological variations of this species. In the western and extreme eastern ranges the calyx tends to be relatively short, whereas in the central and southern ranges it is about as long as the corolla tube. The population considered as ssp. *laniti* seems to be the most distinctive, characterized by the short calyx, the corona puberulent within, the leaves densely puberulent or glabrescent above and the follicles usually

inconspicuously lenticellate. This is a rather uniform population although widely distributed from China to the Philippines through Indochina, Thailand, Malaya and western Indonesia. However, mention should be made of one specimen collected in Vietnam (*Colani 4038*): The few-flowered inflorescence, the corona segments coherent and the relatively long calyx lobes of this specimen approach the characters of *W. annamensis* and I suspect that the 2 hybridize.

Wrightia pubescens ssp. *pubescens* has the calyx lobes as long as the corolla tube, usually recurved at the apex, and puberulent leaves and corona. However, many collections from Timor (type of *W. calycina*), eastern Java and West Irian possess glabrous leaves and corona and provide a link with the population in the central range known as ssp. *candollei*.

Variation within the latter is so extreme that some specimens from the Philippines, with the inflorescence few-flowered and calyx lobes obtuse and auriculate appear to belong to a distinct species (*W. candollei*). Some odd plants have infundibuliform corollas and the anthers included which recall *W. coccinea* of § SCLERANTHERA. However, there are many intermediate specimens which match so closely those of Timor and eastern Java that I am reluctant to assign a specific rank to this population. Finally, this subspecies shows the possibility of hybridization with *W. laevis* to judge from the examination of one specimen (*Vidal 3276*) with the corona laciniate and provided with minute alternating supplementary segments and the flowers relatively small. There is another specimen (*Vidal 1009*) with the pubescent corona which I interpret as a hybrid with ssp. *laniti* with backcross to ssp. *candollei*, for it is closer to the latter.

Within ssp. *penicillata*, the calyx is relatively short and the leaves appear to be usually glabrous, but this variation as well as that of the flower color are within the range of the species. Hence this population does not deserve to be maintained as a distinct species. Finally, ssp. *novobritannica*, although characterized by a short calyx, has features which indicate a close relationship with ssp. *candollei* in the subentire corona segments.

11. WRIGHTIA ANNAMENSIS Eberth. & Duby, Agron. Colon. (Paris) **1**: 38. 1913. (T.: *Eberhardt s. n.*, photo. MO!).

Nerium antidysentericum acc. Lour., Fl. Cochinch. 116. 1790, non L.

Shrubs or rather small trees up to 4 m. tall; branchlets slender, glabrous, the gray-brown bark striate and conspicuously lenticellate. Leaves narrowly elliptic to elliptic, occasionally obovate, caudate-acuminate at the apex, acute to obtuse at the base, 7-12 cm. long, 3-5 cm. broad, membranaceous to chartaceous, glabrous except along the veins beneath, rarely puberulent throughout, the secondary veins 9-12 pairs, impressed above, prominent beneath; petiole about 0.5 cm. long, puberulent. Inflorescence terminal, monochasial, rather lax, almost as long as the subtending leaves; peduncle about 1 cm. long, sparsely puberulent, the bracts narrowly ovate, about 0.3 cm. long; pedicels slender, 0.7-1.2 cm. long, minutely puberulent. Flowers pale greenish or red; calyx lobes ovate, acuminate, about 3 mm. long,

glabrous and ciliolate, bearing within 5 alternate, orbicular or ovate squamellae half as long as the lobes; corolla subrotate, the tube dilated at the insertion of the stamens, more or less constricted at the orifice, about 8 mm. long, minutely puberulent without, the lobes obliquely ovate, acute, 12-16 mm. long, puberulent-papillate; corona coherent at the base and completely adnate to the throat of the corolla tube except the tips of the segments, the antepetalous tridentate and strongly adnate to the blade of the corolla, about 6 mm. long, the alternipetalous bifid, about 4 mm. long; stamens more or less included, inserted within the corolla tube, about 7 mm. long, the anthers more or less exserted, pubescent, the acumen barbate, the filament relatively long, glabrous; carpels 2, coherent, glabrous, about 1.5 mm. long, the style dilated near the subcapitate stigma. Follicles 2, coherent, minutely lenticellate, 15-20 cm. long; seeds linear fusiform, about 1.5 cm. long, the white coma about 4 cm. long.

Vietnam and adjacent China; common in lowlands up to 300 m. elev.; flowering in June, fruiting in August, September.

Vernacular names; *Cay muc bac, Cay long muc.*

CHINA. YUNNAN: vicinity of Yunchow, in light woods, *Liang 70124* (A).

VIETNAM. Bienhoa, Longthanh, *Bon 345* (UC); Hue, in thicket, rich, moist loam, *McClure 7267* (US), P.t. *Ngan 1470, 1821* (SAIG); Quangtri, *Chevalier 41242* (NY); Tourane, foothills to Mt. Bana, roadside near dwelling, *Clemens & Clemens 4124* (A, BM, G, K, MICH, NY, UC, US); vicinity of Tourane, along new road by cabin, *Clemens & Clemens 3367* (A, BM, G, K, MICH, MO, NY, PH, UC, US, W), P. t. *Ngan 1862* (SAIG); W. of Day, between Hanoi and Myduc, *Balansa 4720* (P).

Wrightia annamensis can be mistaken for the more widespread *W. pubescens* particularly in the structure of the corona flower and the coherent follicles. However its monochasial inflorescence as well as its almost glabrous leaves are characteristics which help in separating *W. annamensis* from *W. pubescens ssp. laniti* within its range.

12. WRIGHTIA LANCEOLATA Kerr, Kew Bull. **1937:** 89. 1937. (T.: *Kerr 10926!*).

Shrubs as much as 2 m. high; branches slender, the bark gray to brown, rimose, glabrous, the current year's growth angular, puberulent. Leaves narrowly ovate, long-acuminate at the apex, acute at the base, 5-10 cm. long, 1.5-3.5 cm. broad, chartaceous to coriaceous, puberulent throughout, becoming glabrescent above, except upon the midrib, the secondary veins 15-19 pairs, curved towards the apex, obscure above, prominent beneath; petiole canaliculate, about 0.3 cm. long, puberulent. Inflorescence terminal, aggregate dichasial, few-flowered, about half as long as the subtending leaves; peduncle rather stout, about 0.5 cm. long, puberulent; pedicels about 0.7 cm. long. Flowers red, moderately large; calyx lobes broadly ovate, acute, about 2.5 mm. long, minutely puberulent without, ciliolate, bearing within 5 orbicular to ovate, serrulate squamellae, about half the length of the lobes; corolla subrotate, the tube cylindrical, about 2.5 mm. long, the lobes obovate-elliptic, about 17 mm. long, puberulent-papillate; corona about half the length of the stamens, the antepetalous segments crenulate, almost completely adnate to the

corolla lobes, about 3.5 mm. long, glabrous within, the alternipetalous obsolete; stamens 5, inserted at the orifice of the corolla tube, the anthers sparsely puberulent, the acumen barbate, the filament about 1 mm. long, glabrous; carpels 2, free, glabrous, about 1.7 mm. long, the style slender, slightly dilated near the tip, about 5 mm. long. Follicles 2, coherent, about 15 cm. long; seeds linear-fusiform, about 1 cm. long, the white coma about 3 cm. long.

Endemic to Thailand; flowering in July, fruiting in December.

Thailand. RACHABURI: Sam Roi Yawt, Prachuap, on rocky limestone hill, *Kerr 10926* (A, BM, E, K, L); *Put 2514* (BM, E, L).

Pichon put this species in synonymy under *W. tomentosa*. However, *W. lanceolata* is definitely a very distinctive species characterized by the leaves ovate-lanceolate, long-acuminate, coriaceous with numerous secondary veins, the lack of alternipetalous segments, the corona completely adnate to the corolla lobes and the few-flowered inflorescence. Therefore its relationships are difficult to ascertain and I am unable to determine to which species of *Wrightia* it is most closely related.

13. WRIGHTIA ANGUSTIFOLIA Thwaites, Enum. Pl. Ceylon 193. 1860. (T.: *C. P. 1839, Gardner s. n.*!).

Small trees up to 15 m. high; branchlets slender, terete, glabrous even when immature, the bark rimose, pale gray. Leaves drooping, linear-elliptic to linear-ovate, obtuse at the apex, acute at the base, 7-14 cm. long, 1-2 cm. broad, membranaceous, glabrous throughout or sometimes densely puberulent beneath upon the midrib near the base of the blade, the midrib immersed above, prominent below, the secondary veins 8-13 pairs, arcuate toward the margins; petiole relatively short, 0.2-0.6 cm. long, glabrous, occasionally puberulent. Inflorescence terminal, aggregate dichasial, shorter than the subtending leaves; peduncle slender, about 3 mm. long, glabrous, the bracts scarious, about 1.5 mm. long; pedicels slender, about 8 mm. long. Flowers cream-white, malodorous, relatively small, about 8 mm. long; calyx lobes narrowly ovate, about 1.2 mm. long, ciliolate and glabrous, bearing within 5 linear-lanceolate squamellae; corolla subrotate, the tube cylindrical, about 1.8 mm. long, the lobes narrowly oblong, obtuse, about 6 mm. long and 2 mm. wide, minutely papillate; corona relatively long, glabrous, consisting of 5 alternipetalous segments, bifid or laciniate at the tip, about 5 mm.long and 1 mm. broad; stamens 5, inserted at the orifice of the corolla tube, the anthers sparsely puberulent, the filament relatively slender, about 1 mm. long, glabrous, the basal auricles attenuate, the acumen barbate; carpels 2, free, about 1 mm. long, pubescent at the apex, the common style slender, dilated near the subcapitate stigma. Follicles 2, free, slender and terete, finely striate and sparsely lenticellate, 20-27 cm. long, glabrous; seeds linear, about 1.5 cm. long, the yellowish coma 3.5-4.0 cm. long.

Endemic to Ceylon; confined to the dry zone from Central Province toward North East; flowering in June and July.

Vernacular name: *Velai-pal-madan-kai.*

CEYLON. NORTH CENTRAL PROVINCE: Anuradhapura, *Trimen 35* (UPS); summit of Ritigala, *Willis 104* (UPS). CENTRAL PROVINCE: Dambulla, *C. P. 1839, Gardner s. n.* (BM, G, GH, K, W). PRECISE LOCALITY UNKNOWN: *unknown collector s. n.* (NY).

Wrightia angustifolia can easily be recognized by the relatively small flowers, the linear-lanceolate leaves, the pubescent carpels and the corona consisting of 5 alternipetalous segments as long as the stamens.

14. WRIGHTIA LECOMTEI Pitard in Lecomte & Humbert, Fl. Gén. Indo-chine **3:** 1118. 1933. (T.: *Gourgand s. n.,* photo. MO!).

Small trees up to 5 m. high; branchlets terete, slender, the bark gray to brown, lenticellate, the current year's growth puberulent. Leaves elliptic to obovate, the apex caudate-acuminate, the base acute, 5-8 cm. long, 2.0-3.5 cm. broad, membranaceous, minutely puberulent on both surfaces, the midrib impressed above, prominent beneath, the secondary veins 6-8 pairs, curved towards the apex; petiole canaliculate, 0.2-0.4 cm. long, densely puberulent. Inflorescence terminal, rather lax, aggregate dichasial, about as long as the subtending leaves; peduncle 1.0-1.5 cm. long, puberulent; pedicels slender, 1.5-2.0 cm. long. Flowers white, fragrant; calyx lobes broadly ovate, about 1.8 mm. long, ciliate and puberulent without, bearing within 5 narrowly ovate to ovate squamellae, shorter than the lobes; corolla subrotate, the tube subcylindrical, about 6 mm. long, glabrous, the lobes subobovate, obtuse, about 12 mm. long, minutely puberulent-papillate; corona relatively minute, consisting of 5 alternipetalous segments entire or bifid, about 1 mm. long; stamens 5, inserted at the orifice of the corolla tube, the anthers puberulent without, densely so within, the acumen barbate, the basal lobes slenderly attenuate, the filament about 1.5 mm. long; carpels 2, free, about 1.5 mm. long, glabrous, the style slender, about 7 mm. long, dilated near the subcylindrical stigma. Follicles 2, free, terete-fusiform, about 16 cm. long; seed not seen.

Cambodia to Thailand; flowering in May.

Vernacular name: *Prapech changvâ* (*Cambodia*—Gourgan).

THAILAND. KRUNGTHEP: Bangkok, in hedge zone, *Kerr 10703* (BM, E, L). NAKAWN SAWAN: Me Wong, in mixed forest, *Kerr 6020* (BM, E, K, L). NAKAWN SRITAMARAT: Patalung, *Gwynne-Vaughan 281* (CAL).

This species is closely related to *W. religiosa* and *W. angustifolia.* It differs from the former by the presence of a corona, the corolla lobes subobovate and from the latter in the minute corona, the carpels glabrous and the relatively larger flowers.

15. WRIGHTIA RELIGIOSA (Teijsm. & Binn.) Benth. in Benth. & Hook., Gen. Pl. 2: 713. 1876.

Echites religiosa Teijsm. & Binn., Tijdschr. Ned. Ind. **27:** 34. 1864, ex char.
Wrightia filipendula Pierre in Planchon, Prod. Apoc. 333. 1894, fide Pichon.

Evergreen shrubs reaching a height of 2 m., the branches rather slender, terete, gray, the current year's growth gray to brown-reddish, minutely puberulent. Leaves elliptic to ovate, the apex acute to obtusely acuminate, the base cuneate, 3-7 cm. long, 1.5-2.5 cm. broad, membranaceous, glabrous throughout, occasionally puberulent upon the midrib and veins, the secondary veins 5-7 pairs, arcuate towards the margins; petiole slender, about 0.2 cm. long, puberulent along the edges. Inflorescence terminal, monochasial, rather lax, about as long as the subtending leaves; peduncle rather stout, about 0.5 cm. long, glabrous. Flowers white, occasionally yellow, fragrant, moderately small; calyx lobes ovate, acute, about 1.5 mm. long, ciliate and glabrous, bearing within 5 alternate, narrowly ovate squamellae; corolla subrotate, the tube cylindrical, about 4 mm. long, slightly constricted at the orifice, glabrous, the lobes obovate, obtuse, about 7 mm. long, reflexed or widely spreading, thinly membranaceous, puberulent-papillate; corona obsolete; stamens 5, inserted at the orifice of the corolla tube, the anthers about 4 mm. long, puberulent within, glabrous without, the acumen glabrous, the basal anther lobes slenderly attenuate, the filament slender, about 2 mm. long, glabrous; carpels 2, free, about 1 mm. long, glabrous, the style slender, about 6 mm. long, the stigma subcylindrical, slightly constricted at the median region, terminated by a biapiculate stigma. Follicles 2, free, slender and terete, 12-17 cm. long, smooth, finely striate and glabrous; seeds linear fusiform, about 0.8 cm. long, the white coma about 3.5 cm. long.

Northern Malaya, Thailand, Cambodia and southern Vietnam; common in evergreen forests but also widely cultivated in gardens and around temples; flowering around the year.

Vernacular names: *Mok* (Thailand—Kerr); *Dam prapech changva* (Cambodia—Pitard); *Mai-hoàng* (Vietnam—An).

CAMBODIA. Angkor, *Thorel 2084* (A, K); Kampot, *Geoffray 389* (SAIG, UC); *Gourgaud s. n.* (NY); *Pierre s. n.* (NY); Prek popoul, *Dong phuc Long 243* (SAIG).

INDONESIA. SUMATRA: Riau archipel, Bintan, Penang, probably cultivated, *Bunnemeijer 6534* (L).

MALAYA: Perlis, Kangar, on edges of rice fields, *Henderson S.F.N. 22909* (NY); *Ridley 14949* (BM, SING); Pulau Lankawi, Kuah, *Haniff 15482* (SING); Singapore, cult., *Anderson 115* (CAL); *Maingay 3334* (K); precise locality unknown, *Maingay 1071* (CAL).

THAILAND. CHANTABURI: Rayawng, Ban Pe, *Put 2708* (BM, E, L). KRUNGTHEP: Bangkok, in scrub jungle, *Kerr 3704* (BM, K); Bangkok, no precise data, *Lakshnakara 201* (E); Bangkok, on canal bank, *Marcan 269* (BM, K); in temple gardens, *Marcan 570* (BM, K, MO), *1980* (BM), *2080* (BM); *Schomburgh 132* (CAL); *Zimmermann 24* (BM, G, K, L, MO, US, W), *115* (BM, G, K, L, MO, US, W). NAKAWN SAWAN: Kampengpet, *Kerr 2995* (BM, K); Me Wong common in evergreen forests, *Kerr 6018* (BM, K). NAKAWN SRITAMARAT: Ta Samet, *Kerr 14292* (BM). PAYAP: Chiengmai, *Kerr s. n.* (BM). PRACHINBURI: Ban Sriracha, *Collins 669* (E, K), *825* (BM, K, US), in evergreen forests, *Marcan 1201* (BM). PUKET: Krasom, *Curtis 3241* (SING). SURAT: Champawn, *Haniff & Nur 4356* (K, SING). Precise locality unknown, *Haase s. n.* (BM).

PHILIPPINES. Manila, cult., *Vidal 3247* (K).

VIETNAM: Giadinh, *Lý văn Hôi 1454/Long* (MO); Mt. Lap vo, near Saigon River, *Pierre 3578* (A, K); Phúnhuân, vicinity of Saigon, *An s. n.* (MO); Biên hōa, Trang bom, *Dao dinh Khang s. n.* (SAIG.)

This is the most distinctive species of § WRIGHTIA, with its flowers devoid of a corona. However, by virtue of the structure of its stamens and the shape of its calycine squamellae, *W. religiosa* is most closely related to *W. angustifolia* and *W. lecomtei.*

SECTION 2. **BALFOURIA** (R. Br.) P.t. Ngan, stat. nov.

Balfouria R. Br. in Mem. Wern. Soc. **1:** 70. 1811, as genus.

KEY TO THE SPECIES

a. Leaves elliptic to narrowly elliptic and narrowly ovate; follicles free; flowers relatively large, 12-18 mm. long; corona segments more or less coherent; calycine squamellae 5. Plants of East Africa.

- b. Leaves narrowly ovate, 6-12 cm. long; flowers about 12 mm. long; corolla subrotate, the lobes pubescent within; corona about 2 mm. long; calyx longer than the corolla tube. ....16. W. NATALENSIS
- bb. Leaves elliptic to narrowly elliptic, 1.5-6.0 cm. long; flowers about 18 cm. long; corolla subsalverform, the lobes minutely puberulent-papillate within; corona about 1 mm. long; calyx much shorter than the corolla tube. ....17. W. DEMARTINIANA

aa. Leaves linear-falcate; follicles coherent; flowers relatively small, 6-10 mm. long; corona segments completely coherent into a cupule surrounding the stamens; calycine squamellae 10. Plants of Australia. ....18. W. SALIGNA

16. WRIGHTIA NATALENSIS Stapf, Kew Bull. **1907:** 51. 1907. (T. : *Wood 7861!*).

Small trees up to 15 m. high; branchlets gray to brownish, lenticellate and striate, the current year's growth glabrous. Leaves drooping narrowly ovate, occasionally ovate, the apex acuminate, the base acute, 6-12 cm. long, 1.2-2.0 cm. broad, membranaceous, densely puberulent along the base of the midrib beneath, otherwise glabrous, the midrib slightly elevated above, the secondary veins 12-17 pairs, arcuate toward the margins; petiole about 0.5 cm. long, puberulent. Inflorescence terminal, aggregate dichasial, several-flowered, about half as long as the subtending leaves, puberulent; peduncle 0.5-1.0 cm. long, the bracts linear, 0.5-1.0 cm. long, glabrous, pedicels about 0.7 cm. long. Flowers cream to yellow; calyx lobes narrowly ovate, obtuse, cleft nearly to the base, about 5 mm. long, puberulent without, bearing within 5 oblong, crenulate squamellae, about 0.7 mm. long; corolla subrotate, the tube about 4 mm. long, glabrous, the lobes narrowly ovate to ovate, obtuse, about 7.5 mm. long, papillate without, pubescent within; corona relatively short, the antepetalous segments subtruncate to emarginate, more or less coherent and adnate merely to the base of the corolla lobes, about 2 mm. long, bearing within 2 filiform appendages shorter than the segments; stamens 5, inserted at the orifice of the corolla tube, the anthers glabrous without, pubescent within, the acumen minutely puberulent, the filament definitely longer than the basal anther lobes; carpels 2, free, about 1.5 mm. long, glabrous, the common style about 3.5 mm. long, dilated near the subcapitate stigma. Follicles 2, terete and free, 18-35 cm. long, striate; seeds linear, about 1.7 cm. long, the white coma about 4.5 cm. long.

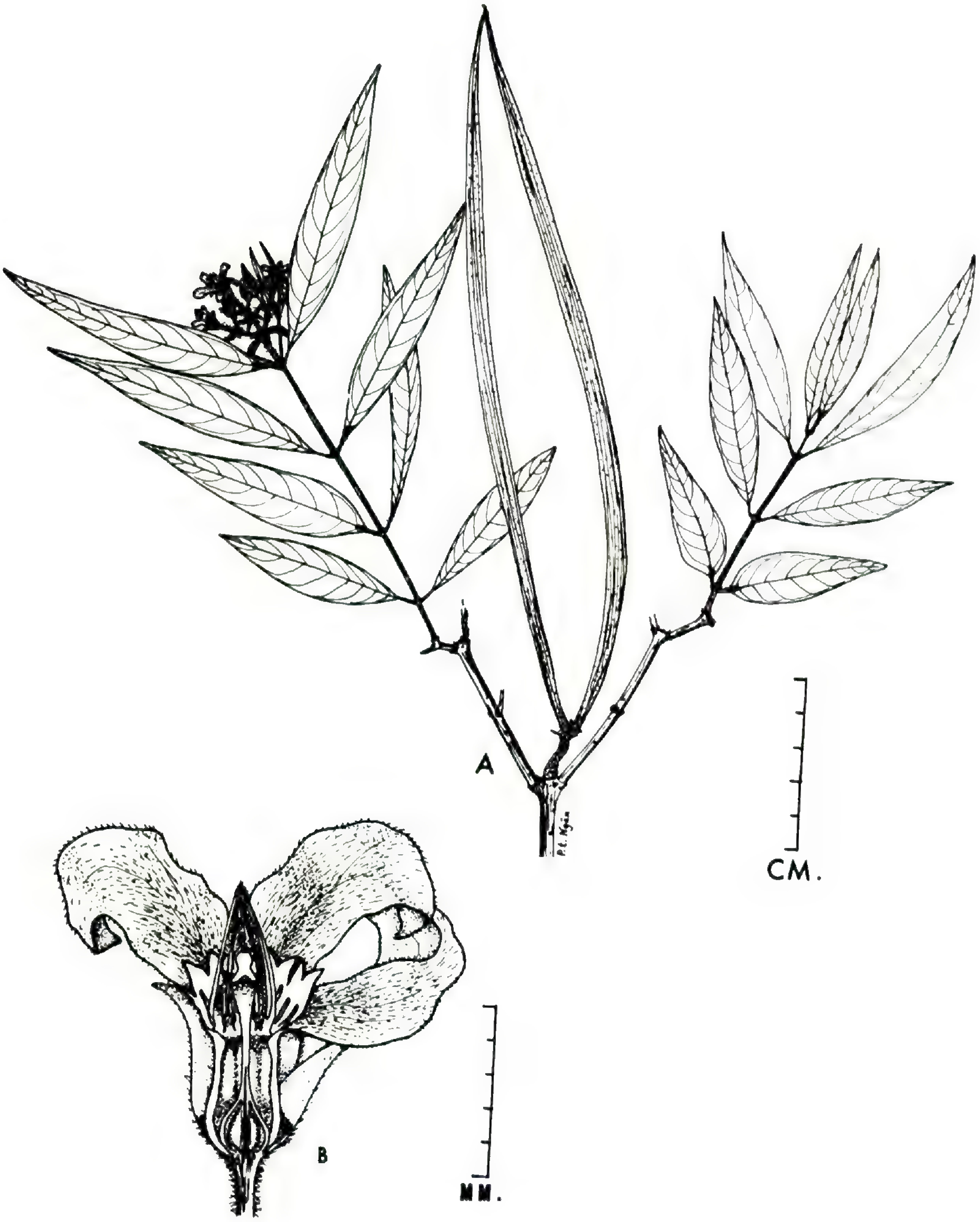


Figure 10. *Wrightia natalensis* Stapf; A, twig with inflorescences and follicles; B, longisection of the flower.

Endemic to southern Mozambique and northeastern Union of South Africa; in mixed bush, wooded grassland on sandy or rocky soil; flowers from August to November, follicles from November to June.

Vernacular names: *M'tsatsala* (Mozambique—Gomes e Sousa); *Mohlazi osa se Bôikgo* (Sekukuniland—Barnard); *Umkhontompuzane* (Zuzuland—Tinley).

MOZAMBIQUE. Maputo distr.: in bushland of Catuan, *Hornby 2625* (K, PRE, SRGH); S. Lourenço Marques distr.: Santaca, in open forests, on sandy argillous soil, *Gomes e Sousa 3791* (PRE).

S. AFRICA. NATAL: Hlabisa distr.: False Bay, *Bayer 20* (PRE); *Ward 1633* (K, PRE, UPS), *2526* (PRE), *3576* (PRE); Ingwavuma distr.: Nduma game reserve, Zuzuland, in open Albizzia wooded growth grassland, on hard red loamy soil, *Tinley 411* (PRE, SRGH); Ndwandwe distr.: Umzinyati Falls, *Wood 7861* (K), *11530* (F, G, PRE); *Haygarth & Wood 12253* (K); Pietermaritzburg; Umgeni valley near Nagle Dam, *Cheadle 627* (PRE, SRGH); Lower Tugela distr.: bottom of Tugela valley, below Bulwer farm, *Edwards 1875* (PRE). TRANSVAAL: Sekukuniland: Lydenburg, *Barnard 429* (PRE), *Moffatt 29092* (PRE); Sibasa distr.: Punda Milia, *Lamont 52* (PRE); Zoutpansberg distr.: N. of Fogwells, *Smuts & Gillett 3111* (PRE); Wylliesport, in mixed bush on steep, rocky hill side, *Codd & Dyer 3925* (MO, PRE), *Dyer 4326* (MO), *Pole Evans 3421* (MO), *3524* (MO, PRE, SING); Wambia: Kruger National Park, in thick bush on sandveld, *Schÿff 4107* (K, PRE, SRGH, UPS).

SWAZILAND. *Millet S/58* (PRE).

Wrightia natalensis surely is the most distinctive species of the genus with the corolla lobes conspicuously pubescent within, the emarginate corona segments with 2 filiform appendages within and the narrowly ovate calyx lobes longer than the corolla tube.

17. WRIGHTIA DEMARTINIANA Chiov., Ann. Bot. Roma **13:** 405. 1915. (T.: *Paoli 839!*).

Piaggiaea demartiniana (Chiov.) Chiov., Fl. Somala **2:** 290. 1932.
Piaggiaea boranensis Chiov., Miss. Biol. Borana, Racc. Bot. Angiosp.-Gymnosp. 159. 1939. (T.: *Cufodontis 86!*).
Wrightia boranensis (Chiov.) Cuf., Bull. Jard. Bot. État Brux. **30**, Suppl.: 692. 1960.

Deciduous shrubs or small trees up to 10 m. high; branches usually crooked, smooth, gray to brownish, the current year's growth relatively short, puberulent. Leaves elliptic to narrowly elliptic, occasionally obovate, the apex obtuse, the base acute, 1.5-6.0 cm. long, 0.4-1.0 cm. broad, membranaceous, puberulent, the midrib slightly prominent beneath, the secondary veins 6-9 pairs, arcuate; petiole 0.2-0.4 cm. long, puberulent. Inflorescence terminal, aggregate dichasial, as long as the subtending leaves, puberulent; peduncle 0.1-0.2 cm. long, the bracts narrowly ovate to ovate, about 0.2 cm. long; pedicel relatively slender, about 0.5 cm. long. Flowers white or cream, fragrant; calyx lobes ovate, about 2 mm. long, puberulent without, ciliate, bearing within 5 ovate, acute squamellae, as long as the lobes; corolla subsalverform, the tube subcylindric, slightly dilated at the base, constricted at the orifice, about 7 mm. long, puberulent without, the lobes narrowly obovate, obtuse, about 10 mm. long, puberulent-papillate; corona relatively short, about 1 mm. long, the antepetalous and alternipetalous segments crenulate to slightly dentate, more or less coherent, adnate merely to the base of the corolla lobes; stamens 5, inserted

at the orifice of the corolla tube, the anthers glabrous without except near the tip, puberulent within, the acumen barbate, the filament as long as the basal anther lobes; carpels 2, free, glabrous, the common style gradually dilated near the subcapitate stigma head. Follicles 2, terete-fusiform, 13-30 cm. long, finely striate; seeds linear, about 2 cm. long, the coma white to dull yellow, about 3.5 cm. long.

Endemic to Somalia, southeastern Ethiopia and northern Kenya; in wooded steppe on red sandy soil; lowlands up to 1000 m. elev.; flowers from September to March, follicles from March to October.

Vernacular names: *Habrota* (Boran—Dale); *Maiyu* (Boran—Gillett); *Rabban* (Boran—Gillett); *Silchacho* (Kenya—Adamson); *Haiyo* (Somalia—Hemming).

ETHIOPIA. OGADEN: Wardere, in open Acacia-Commiphora on red sandy soil, *Hemming 372* (EA, FI); in medium density thorn bush, *Simmons 2* (EA), *58* (EA); 53 miles E. of Wardere, *Hemming 1515* (EA); Locust camp ground, Wardere, *Barnes 11960* (EA).

KENYA. NORTHERN FRONTIER PROVINCE: 16 km. N. of Archers Post, *Dale k776* (EA, FI); Dandu, in rich Commiphora-Acacia scrub on red sandy soil, *Gillett 12530* (BM, EA, FI, G, PRE); Garissa area, *McLoughlin s. n.* (EA); Isiolo-Maraabit, on rocky outcrop with Commiphora, Grewia, Tephrosia, *Verdcourt & Dale 2212* (EA); Kiliwa Hevi Police Post, Mandera, *Adamson 77* (EA, PRE).

SOMALIA. Borana, Malca Guba sul Daua-Parma, *Cufodontis 86* (FI); 20 km. W. of Bur Acaba, *Bond & Pechanee 2* (EA); Cisjuba, Salagle, *Tozzi 264* (FI); Dinsor, on rocky hill side, *Bally B9334* (EA); between Dorianle and Oneiatha, *Paoli 896* (FI); along Giuba River near Biobahal, *Paoli 851* (FI); Guiba River near Matagassile, *Paoli 839* (FI); near Matagoi, *Paoli 680* (FI).

This species is easily distinguished from the related species within § *Balfouria* by the subsalverform corolla and the small corona with both antepetalous and alternipetalous segments and the relatively small leaves.

18. WRIGHTIA SALIGNA (R. Br.) F. Muell. ex Benth., Fl. Austr. **4:** 316. 1869.

Balfouria saligna R. Br. ex A. DC. in DC., Prodr. **8:** 467. 1844. (T.: *Brown 2865!*).

Shrubs or small trees up to 7 m. high; branches terete, very slender, the bark rough, gray to brownish, glabrous. Leaves drooping, linear-falcate, occasionally linear-ovate, the apex acuminate, the base attenuate, narrowly decurrent to the indefinite petiole 8-12 cm. long, 0.3-1.5 cm. broad, coriaceous, glabrous, the midrib obscure above, prominent beneath, the secondary veins numerous but usually inconspicuous. Inflorescence terminal, aggregate dichasial, about one-fourth the length of the subtending leaves; peduncle 1-2 cm. long, glabrous to minutely puberulent, the bracts linear, about 0.4 cm. long; pedicel about 1 cm. long, puberulent. Flowers yellow, relatively small; calyx lobes ovate, acute, about 1.5 mm. long, minutely puberulent without, ciliate, bearing within 10 glandular squamellae, half as long as the lobes; corolla subrotate, the tube 2-3 mm. long, glabrous, the lobes subobovate, obtuse to acute, 4-7 mm. long, puberulent-papillate; corona about 2.5 mm. long, the antepetalous segments adnate merely to the base of the corolla lobes and coherent into a truncate and crenulate cup around the stamens; stamens 5, inserted at the orifice of the corolla tube, the anthers sparsely puberulent within,

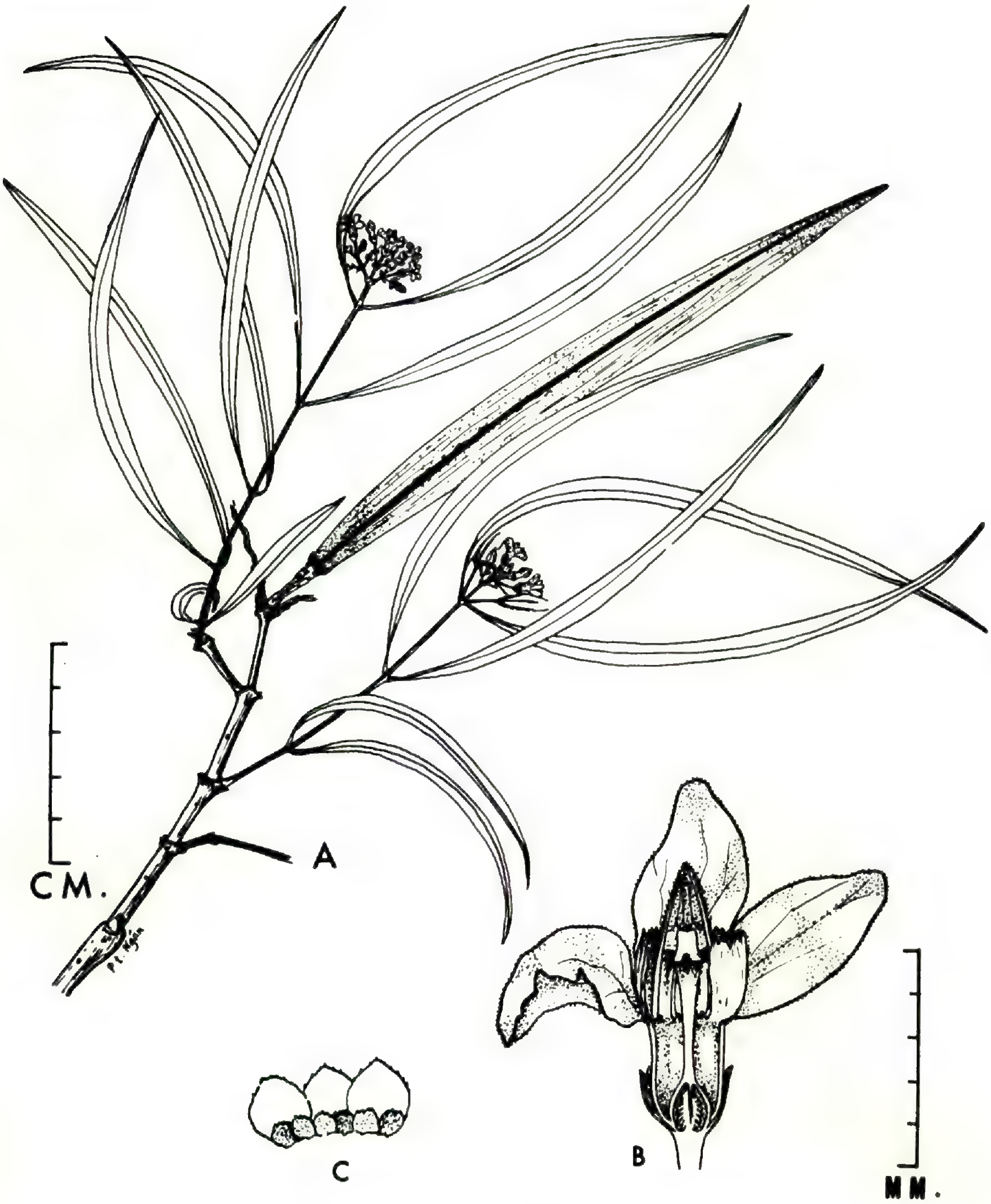


Figure 11. *Wrightia saligna* (R. Br.) F. Mueller ex Benth.; A, twig with inflorescences and follicles; B, longisection of the flower; C, calyx lobes and squameliae.

pubescent without, the acumen barbate, the filament as long as the basal anther lobes; carpels 2, coherent, glabrous, the style gradually dilated near the subcapitate stigma head. Follicles 2, coherent, 15-20 cm. long; seeds linear-fusiform, relatively few in number, 1.0-1.5 cm. long, the white coma about 3.5 cm. long.

Endemic to northern and northeastern Australia, in mixed open forest of Eucalyptus, on sandy and rocky soil; flowers from September to May, ripe follicles from May to October.

Vernacular name: *Coolaroo,* "milk bush" (W. Australia—Rust)

Australia. northern territory: Bickerton Island, South Bay, common in Eucalyptus spenceriana woodland on granite outcrop, *Spetch 602* (BRI, CANB); Borroloola, *Hill 660* (MEL, NSW); Oenpelli, in mixed open forest on sandy outwash plain, *Spetch 1267* (BRI, CANB, MEL, NSW, US); *Blake 16994* (BRI); Port Darwin, *Bleeser 545* (MEL, NSW); *Holtze 583* (MEL), *916* (MEL), *s. n.* (NSW), *Schultz 542* (MEL); Wearyan River, Manangoora, *Travers 9061* (NT); precise locality unknown: *Hill 451* (MEL), *unknown collector 1019* (MEL). queensland: Burke: Bentinck Island, *Bailey s. n.* (BRI), *Henne s. n.* (MEL); Croydon, *Wilson s. n.* (BRI); Kimberley, Carpentaria, *Galliver 37* (MEL); 24.6 mi. N. Lawn Hill station, on stony slope with E. brevifolia and Triodia, *Perry 1106* (BRI, CANB, MEL, NSW, NT, US); Sweers Island, *Henne s. n.* (MEL); 6 mi. W. of Westmoreland station, near creek with E. argillacea, *Perry 1324* (CANB, NT, US). *Cook*: From Cooktown to Gilbert & Flinders rivers, *Palmer 40* (BRI); Daintree, *Mueller s. n.* (MEL); Emuford, near Irvinebank, *Flecker s. n.* (BRI); Endeavour Strait, *Persieh 1033* (MEL); Gilbert River, *Wildash s. n.* (BRI); Thursday Island, *Bailey 5* (BRI), *Podenzana s. n.* (BM); Walsh River, Miller 6 (BRI, NSW). *N. Kennedy:* near junction of Broughton & Burdekin rivers, near Charters Towers, in Eucalyptus forest, on stony brown soil, *Hubbard & Winders 6983* (A, BRI, G, L, W); Burdekin River, *Michael 1503A* (E); Carpentaria Island, *Brown 2865* (E, MEL, MO); near Charters Towers, *Blake 14669* (BRI); lake of Elphinstone, Amalia distr., *Mueller 1663* (MEL); Port Denison, Edgecombe Bay, *Fitzalan 17519* (BM), *s. n.* (MEL), *Mueller s. n.* (GH, L, MEL, NY, W), *unknown collector s. n.* (L, UPS, W). Ravenswood, *Blake 14848* (BRI). *S. Kennedy*: Suttor River, *Mueller 126* (MEL); without precise locality: *Armit 542* (MEL), *837* (MEL), *Bauer s. n.* (W), *Brown s. n.* (G), *Michael 1631* (BRI), *Mueller s. n.* (MEL), *Schomburgk s. n.* (US, W), *Webb 5109* (CANB). w. australia: Cambridge Gulf, *Wright s. n.* (MEL); Denham River, *Fitzgerald s. n.* (NSW), *Staer s. n.* (E); Karunjie station, Kimberley, *Rust 75* (CANB), *51K* (CANB), *176* (CANB); King River, *Fitzgerald s. n.* (NSW), *Staer s. n.* (E); Kings Sound, *Troggat s. n.* (MEL, NSW); Roebuck Bay, *Mueller 73* (MEL).

The linear-falcate leaves and the corona segments coherent into a cup about the stamens at once easily separate this species from all others of the genus. R. Brown and A. De Candolle put *W. saligna* in a distinct genus—*Balfouria;* however, the structure of the seed and flower of this species is unmistakably that of the genus *Wrightia*.

SECTION 3. WALLIDA A. DC. in DC., Prodr. **8:** 404. 1844

Wallida Pichon, Not. Syst. **14:** 87. 1951, as genus.

19. Wrightia antidysenterica (L) R. Br., Mem. Wern. Soc. **1:** 73. 1811. (T.: *Hermann s. n., Koenig s. n.*).

Nerium antidysentericum L., Sp. Pl. 209. 1753, ex char.
Nerium zeylanicum L., Centur. Pl. **2:** 12. 1756, ex char.
Wrightia zeylanica (L.) R. Br., Mem. Wern. Soc. **1:** 73. 1811.
Wallida antidysenterica (L.) Pichon, Not. Syst. **14:** 88. 1951.

Small shrubs as much as 2 m. high; branchlets gray to dark brown, lenticellate and glabrous. Leaves obovate to elliptic, occasionally narrowly elliptic, acuminate to caudate-acuminate at the apex, acute at the base, 3-10 cm. long, 1.5-3.5 cm. broad, membranaceous to subcoriaceous, glabrous even when immature, the midrib more or less elevated above, prominent beneath, the secondary veins 6-9 pairs, arcuate, sometimes obscure above, conspicuous beneath; petiole 2-3 mm. long, glabrous to minutely puberulent. Inflorescence terminal, monochasial, about as long

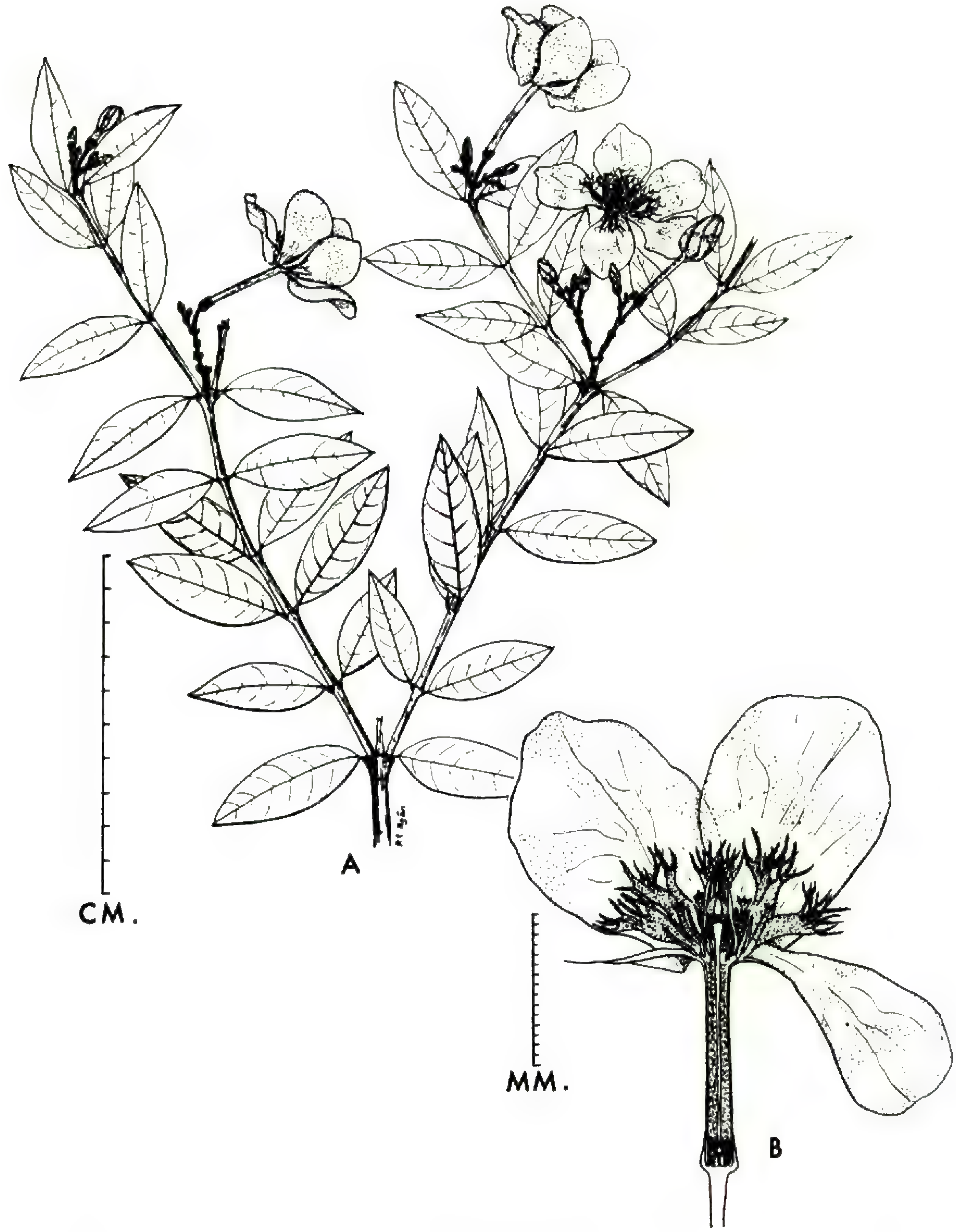


Figure 12. *Wrightia antidysenterica* (L.) R. Br.; A, twig with inflorescences; B, longisection of the flower.

as the subtending leaves, glabrous peduncle rather stout, the bracts minute and scarious; pedicels about 1 cm. long. Flowers white, fragrant; calyx lobes ovate, 3.0-3.5 mm. long, glabrous and ciliate, bearing within 5 alternate, ovate squamellae about 0.8 mm. long; corolla salverform, the tube slender, 17-28 mm. long, glabrous without, puberulent within, the lobes obovate, obtuse, 15-25 mm. long, puberulent-papillate; corona minutely puberulent throughout, consisting of 3 series of segments, the antepetalous multifid, strongly adnate to the corolla lobes, the alter-

nipetalous multifid, shorter, and the alternating supplementary geminate, simple or compound; stamens 5, inserted at the orifice of the corolla tube, the anthers glabrous without, pubescent within, the basal lobes slenderly attenuate, longer than the filament, the acumen glabrous; carpels 2, free, glabrous, about 1 mm. long, the style very long and slender, gradually dilated near the subcapitate stigma. Follicles 2, free, sometimes coherent at the tips, terete-fusiform, 7-15 cm. long; seeds linear, about 1 cm. long, the white coma about 2.5 cm. long.

Endemic to Ceylon; flowering from March to August.

Vernacular names: *Sooddoo-idda* (Thwaites); *Wal-idda* (de Silva).

CEYLON. Colombo, *Meebold 2975* (G), *10849* (CAL), *de Silva 11* (NY), *C. P. 1825, Thwaites* (BM, CAL, G, GH, K, UPS, W); *unknown collector s. n.* (CAL); Galle, *Gardner 557* (BM, K); Kalaeliya, *Simpson 9886* (BM); Kalutara, *Schiffner 2421* (A, L); Kandy, *Moon s. n.* (BM); without precise locality, *Beddome 5123* (BM); *unknown collector s. n.* (G), *Macrae 125* (BM), *Walker s. n.* (K), *Walpietze 56* (L), *104* (G), *s. n.* (L).

This species is so distinct that little can be said about its relationships. The structure of its corona suggests an affinity with *W. tinctoria* of § *Wrightia.*

SECTION 4. **SCLERANTHERA** (Pichon) P.t. Nagan, stat. nov.

Scleranthera Pichon, in Not. Syst. **14**: 88. 1951, as genus.

KEY TO THE SPECIES

a. Leaves glabrous even when immature; inflorescence glabrous; flowers very small, about 7 mm. long; corolla tube appendiculate within; anthers glabrous without. Plants of Palawan (Philippines). .... 20. W. HANLEYI
aa. Leaves puberulent, at least upon the veins beneath; inflorescence minutely puberulent; flowers relatively large, 16-40 mm. long; corolla tube exappendiculate within; anthers pubescent without.
  b. Corolla infundibuliform, the tube definitely campanulate, shorter than to about as long as the calyx; stamens inserted near the orifice of the corolla tube, the anthers half exserted.
    c. Flowers about 1.6 cm. long; alternipetalous corona segments present, the antepetalous trilobed, about ⅓ the width of the corolla lobe; calyx lobes long-acuminate, not auriculate; carpels free. Plants of Burma .... 21. W. COLLETTII
    cc. Flowers 2.0-3.5 cm. long; alternipetalous corona segments obsolete, the antepetalous crenulate, as broad as the corolla lobe; calyx lobes acute to obtuse, usually auriculate; carpels coherent. Plants of East Pakistan, eastern India and adjacent China. .... 22. W. COCCINEA
  bb. Corolla subinfundibuliform, the tube usually more or less constricted at the orifice, 2 to 4 times longer than the calyx; stamens inserted near the base of the corolla tube, the anthers included or slightly exserted. .... 23. W. DUBIA

20. WRIGHTIA HANLEYI Elmer, Leafl. Philipp. Bot. **4**: 1465. 1912. (T.: *Elmer 12873*!).

Small shrubs up to 2 m. high; branches terete, slender, the bark rimulose, gray to brownish, the current year's growth glabrous. Leaves narrowly elliptic to elliptic or oblong-elliptic, occasionally ovate or obovate, the apex acuminate to

mucronate, the base broadly acute to obtuse, 6-15 cm. long, 2-6 cm. broad, coriaceous to chartaceous, glabrous throughout, the midrib canaliculate above, prominent beneath, the secondary veins 7-10 pairs, arcuate towards the margins; petiole canaliculate above, about 0.5 cm. long, glabrous. Inflorescence terminal, monochasial, much shorter than the subtending leaves; peduncle about 0.5 cm. long, glabrous, the bracts minute, scarious; pedicels rather short, about 0.3 cm. long, glabrous. Flowers yellow, small about 7 mm. long; calyx lobes ovate, about 2 mm. long, ciliate and glabrous, bearing within 5 alternate, glandular squamellae much smaller than the lobes, corolla subinfundibuliform, the tube campanulate, appendiculate within, about 3 mm. long, the lobes subovate, acute, about 4 mm. long, puberulent-papillate; corona reddish, the antipetalous segments nearly as large as, and strongly adnate to, the corolla lobes, the alternipetalous reduced to 5 small appendages about 1 mm. long; stamens 5, inserted at about half way within the corolla tube, the anthers 3-5 mm. long, glabrous without, the acumen minutely puberulent, the filament as long as the subtruncate, basal anther lobes; carpels 2, free, glabrous, the style slender, gradually dilated near the subcapitate stigma. Follicles 2, free, terete-fusiform, pendent, 15-20 cm. long; seeds linear-fusiform, about 1 cm. long, provided with a white coma about 3.5 cm. long.

Endemic to the islands of Palawan (Philippines); in clearings, thickets and open forests at low altitudes, on compact gravelly soil; flowering from March to May.

PHILIPPINES. PALAWAN: Puerto Princesa, Mt. Pulgar, *Elmer 12873* (BM, E, F, G, GH, K, L, MO, US, W); Taytay, *Merrill 9373* (BM, F, K, L, MO, NY, SING, US); without precise locality, *Bur. Sci 849,* Foxworthy (NY, US).

Wrightia hanleyi is easily distinguished from the other species of § *Scleranthera* by its glabrous branchlets, leaves and inflorescences, its relatively small flowers and its appendiculate corolla tube.

21. WRIGHTIA **COLLETTII** P.t. Ngan, sp. nov.

Verisimiliter frutices vel arbusculae ramulis juvenalibus dense pubescentibus. Foliorum lamina membranacea elliptica vel obovato-elliptica apice abrupte caudato-acuminata basi cuneata pubescens costa superne impressa subtus prominente nervis secundariis 10-15 partibus. Inflorescentia terminalis monochasialis foliis brevior; pedicellus ca. 0.5 cm. longus puberulusque; calycis laciniae ovatae acuminatae ca. 4 mm. longae extus puberulae intusque basi squamellis alternis praeditae; corolla infundibuliformis tubo campanulato ca. 4 mm. longo lobis subobovatis ca. 12 mm. longis puberulo-papillatis coronae squamis biseriatis glabris basi connatis antepetalis tridentatis ca. 3 mm. longis alternipetalis brevioribus bifidis; stamina prope faucem inserta antheris plus minusve exsertis sagittatis ca. 6 mm. longis utrinque minute puberulis; carpella libera ca. 1.5 mm. longa glabra. Folliculi ignoti. HOLOTYPUS: *Collett* 445 (K).

Endemic to Burma.

BURMA. UPPER BURMA: Shan Hills Terai, 3500 ft. in elev., *Collett 445* (CAL, K).

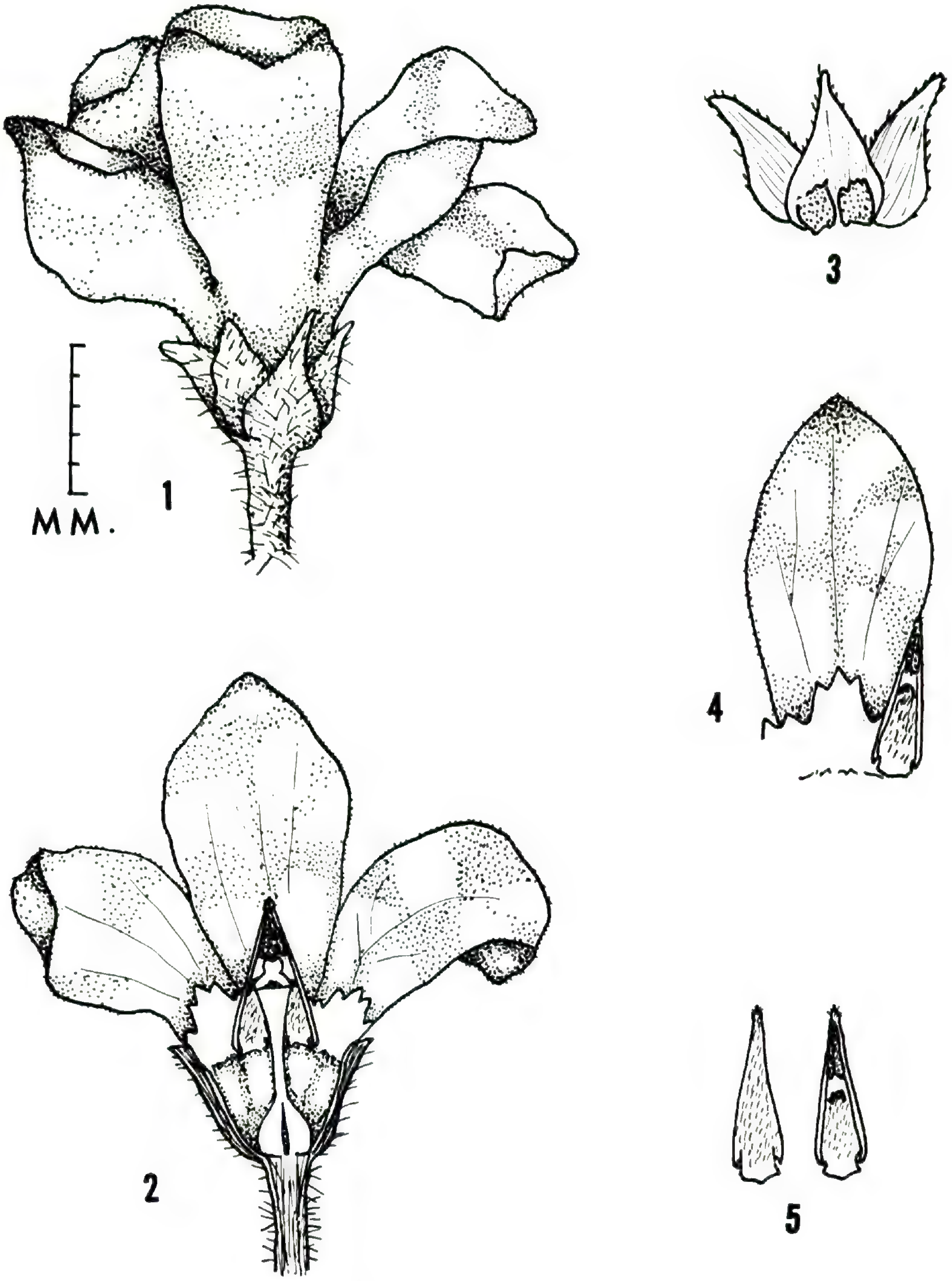


Figure 13. *Wrightia collettii* P. t. Ngan; 1: flower; 2: flower longitudinally opened, showing corona, stamens and ovary; 3: calyx lobes and squamellae; 4: corolla lobe with corona segments and stamen; 5: stamens.

Wrightia collettii is closely related to *W. coccinea* and *W. dubia;* however it is easily distinguished by its relatively smaller flowers and its tridentate antepetalous corona segments. The type specimen is in very poor condition, but the structure of the flower is so unusual that I do not hesitate to consider it as a distinct species even on the basis of a single collection.

22. Wrightia coccinea (Roxb.) Sims, Bot. Mag. **53:** *pl. 2696.* 1826, non Soland. ex Naudin (1852). (T. : *Wallich, cat. n. 1626!*).

Nerium coccineum Roxb., Fl. Ind. ed. Carey & Wall. **2:** 2. 1824.

Shrubs or small trees up to 20 m. high; branchlets ascending, terete, the bark pale gray to brownish, glabrous and lenticellate. Leaves elliptic to ovate, caudate-acuminate at the apex, obtuse to acute at the base, 9-15 cm. long, 3.5-7.0 cm. broad, membranaceous, glabrous throughout, except upon the veins beneath, occasionally puberulent, the secondary veins 8-14 pairs, parallel and arcuate toward the margins, immersed above, prominent beneath; petiole 0.3-0.6 cm. long, puberulent. Inflorescence terminal, dichasial, few-flowered, about half as long as the subtending leaves; peduncle relatively stout, about 0.3 cm. long, puberulent, the bracts foliaceous, up to 2 cm. long, glabrous; pedicels stout, relatively short, about 0.5 cm. long, puberulent. Flowers dull red within, greenish without, fragrant, relatively large; calyx deeply 5-lobed, the lobes broadly ovate, obtuse at the apex, usually auriculate at the base, 5-9 mm. long, glabrous and ciliate, the 5 alternate, ovate squamellae much smaller than the lobes; corolla infundibuliform, the tube campanulate, shorter than the calyx, glabrous, the lobes broadly obovate, subacute to obtuse, puberulent-papillate; corona crimson, about 5 mm. long, shorter than the stamens, the antepetalous segments relatively broad, coherent at the base, crenulate and strongly adnate to the corolla lobes, the alternipetalous segments obsolete; stamens 5, inserted near the orifice of the corolla tube, the anthers about 10 mm. long, sparsely puberulent to glabrous, within, densely pubescent without, the acumen barbate, the filament relatively broad, about 2.5 mm. wide, glabrous within, pubescent without; carpels 2, free, glabrous, about 2 mm. long, the style columnar, abruptly dilated near the subcapitate stigma. Follicles 2, free, about 30 cm. long, very conspicuously lenticellate; seeds linear, about 2 cm. long, the white coma 3.5-4.0 cm. long.

East Pakistan, West Bengal, Assam and Yunnan; in mixed forests and thickets on mountain slopes from 300 to 1800 m. elev.; flowering from April to June, fruiting from June to September.

Vernacular names: *Panal* (Assam—unknown collector); *Pullum* (East Pakistan—Roxburgh); *Khirra* (W. Bengal—Cowan).

China. yunnan: Fo hai, in mixed forests, *Wang 73943* (A); I wu, *Henry 13574* (K, NY); Nan chiao, mountain slope, in forests, *Wang 75279* (A); top of mountain, in thicket, *Wang 75412* (A).

India. assam: Abor Hills, Barlek, *unknown collector 36958* (CAL.) eastern himalaya: Birick, *Cave s. n.* (CAL); Mungkoo Riang road, *Cousins 39* (CAL). sikkim: precise locality unknown, *Anderson s. n.* (CAL); *Cave 6656* (CAL). uttar pradesh: Dehra Dun, cult.,

Kirat Ram s. n. (A); Saharanpur Botanic Garden, *King s. n.* (CAL), *unknown collector s. n.* (CAL). WEST BENGAL: Darjeeling, *Cowan s. n.* (E, US). PRECISE LOCALITY UNKNOWN: *unknown collector s. n.* (CAL).

PAKISTAN. Calcutta Botanic Garden, *Wallich cat. n. 1626a* (BM), *1626B* (G); Tista, Rangpur distr., *Cave s. n.* (E, G), *Clarke 7164* (BM); Sylhet, *Wallich cat. n. 1626* (K), *1627C* (G), *unknown collector s. n.* (CAL).

In his original description Roxburgh cited no specimen, however he mentioned the plant brought from Sylhet to the Calcutta Botanic Garden. In 1823, Wallich sent specimens to Glasgow Botanic Garden under the catalogue number 1626; for this reason I have chosen that specimen as the provisional lectotype.

This species is easily distinguished by its calyx lobes auriculate at the base, glabrous and longer than the tube, its foliaceous, glabrous bracts and bracteoles and its corona with 5 relatively large antepetalous segments.

23. WRIGHTIA DUBIA (Sims) Spreng., Syst. Veg. ed. 16, **1:** 638. 1825.

Cameraria dubia Sims in Curtis, Bot. Mag. **39:** *pl. 1646.* 1814, ex. ic. & char.
Strophanthus jackianus Wall., Cat. no. 1643. 1828, nom. nud.
Wrightia cambodiensis Pierre ex Pitard in Lecomte & Humbert, Fl. Gén. Indochine **3:** 1184. 1933. (T.: *Pierre 4402*!).
Wrightia dubia var. *membranifolia* King & Gamble, Jour. As. Soc. Beng. **74:** 2466. 1907. (T.: *Curtis 2915*!).
Wrightia rubriflora Pitard in Lecomte & Humbert, *loc. cit.* 1185. 1933. (T.: *Hayata s. n., Poilane 5955,* photos. MO!).
Scleranthera cambodiensis (Pierre) Pichon, Not. Syst. **14:** 89. 1951.
Scleranthera dubia (Sims) Pichon, Not. Syst. **14:** 90. 1951.

Shrubs up to 3 m. high; branchlets slender, terete, glabrous to minutely puberulent, the bark gray to brownish, minutely striate and lenticellate. Leaves narrowly elliptic to elliptic or narrowly obovate to obovate, the apex acuminate to caudate-acuminate, the base acute to obtuse, 9-20 cm. long, 2.5-8.0 cm. broad, membranaceous to chartaceous, glabrous to more or less sparsely puberulent along the midrib above, puberulent beneath especially along the nerves, occasionally becoming glabrous, the midrib immersed above, conspicuously elevated beneath, the secondary veins 8-10 pairs, oblique and arcuate toward the margins; petiole canaliculate, 0.3-0.5 cm. long, puberulent. Inflorescence terminal, monochasial, few-flowered, rather condensed, shorter than the subtending leaves, glabrous to minutely puberulent; peduncle about 0.5 cm. long, the bracts ovate, about 0.3 cm. long, scarious; pedicels rather slender, about 0.7 cm. long. Flowers pink, yellow, orange to dull red within, white to yellowish or greenish without, fragrant; calyx lobes narrowly to broadly ovate, 2.5-6.0 mm. long, glabrous or sparsely puberulent, bearing within 5 orbicular to ovate squamellae; corolla subinfundibuliform, the tube suburceolate to campanulate, 6-12 mm. long, minutely puberulent without, the lobes obliquely ovate and acute to ovate-lanceolate, long-acuminate, 16-22 mm. long, minutely puberulent without, glabrous within; corona relatively short and inconspicuous, glabrous, the antepetalous segments reduced to a thickened, triangular ridge completely adnate to the base of the corolla lobes, 2-3 mm. long, the alternipetalous segments entire and obtuse, about 1 mm. long; stamens 5, inserted

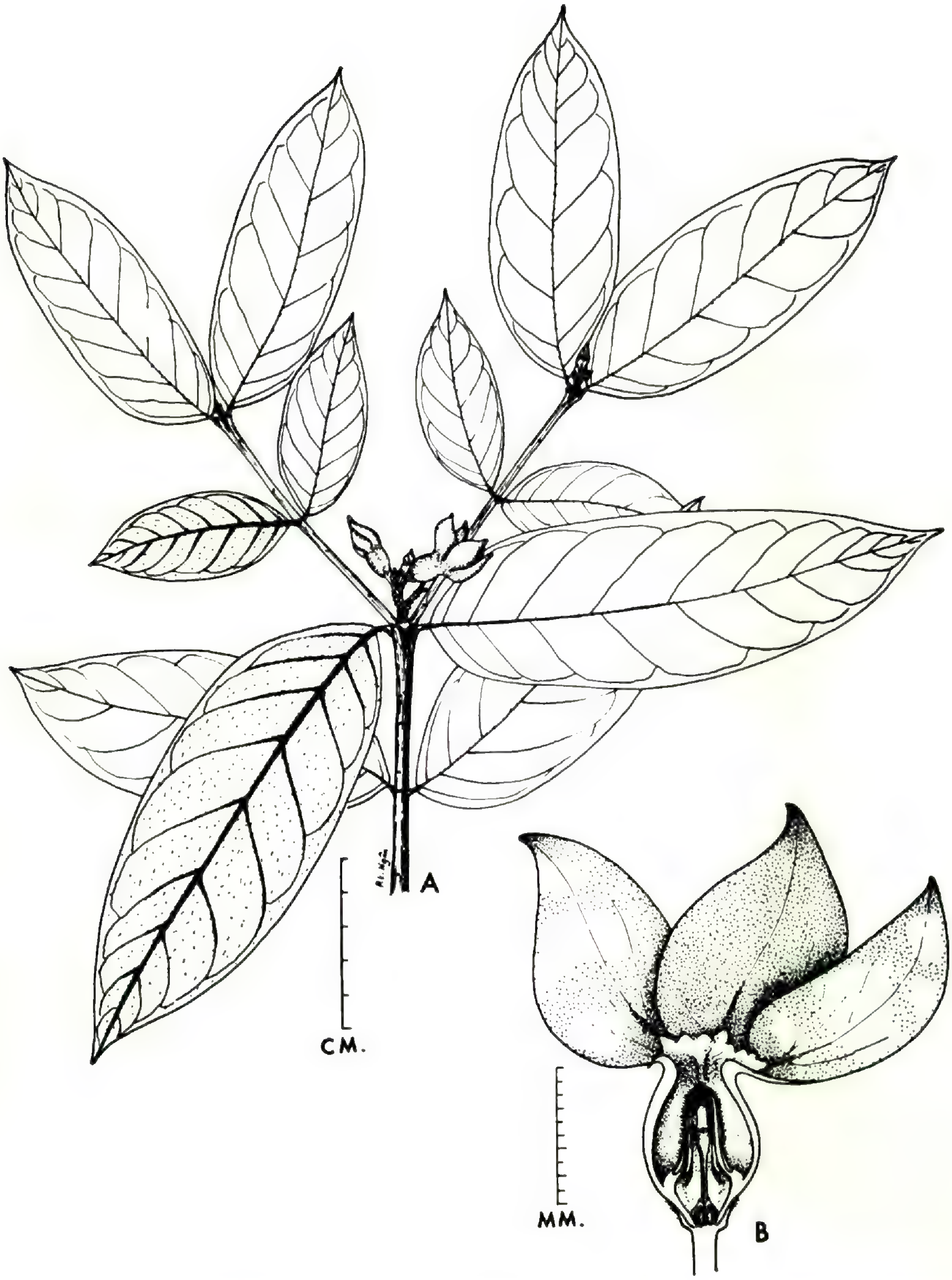


Figure 14. *Wrightia dubia* (Sims) Spreng.; A, twig with inflorescences; B, longisection of the flower.

near the base of the corolla tube, the anthers included or with the tip slightly exserted, about 6 mm. long, sparsely puberulent within, densely pubescent without, the acumen barbate, the filament very broad at the base, glabrous and conspicuously inflexed; carpels 2, free, glabrous, about 1.5 mm. long, the common style gradually dilated near the conical stigma. Follicles 2, free and usually coherent at the tips, slender and terete, about 32 cm. long; seeds linear-fusiform, about 1.5 cm. long, the white coma about 4 cm. long.

Northern Malaya, southern Thailand, Cambodia and southern Vietnam; in bamboo forests, evergreen forests, savannas, on sandy soil, limestone, by stream or along roadside; flowering from November to August.

CAMBODIA. Mont Tamire, Samrong tong, *Pierre 4402* (NY).

MALAYA. KEDAH: Ara Kudah by Sungei krai bridge, *Ridley s. n.* (SING); Kaki Bukit, *Kiah s. n.* (A, L, SING); Telok Apau, Pulau Langkawi, *Haniff 7086* (SING); Yan, *Ridley 5521* (SING). PULAU PENANG: Tanjong Tokong, *Haniff 296* (UC); Telok Bahang, *Curtis 188* (CAL, SING); valley near stream below Waterfall Gardens, *Sinclair, S.F.N. 39023* (SING). SINGAPORE: Botanic Garden, *Nur, S.F.N. 35471* (L).

THAILAND. PUKET: Ban Takuapa, *Kerr 17105* (BM, K, L); Krabi, Tambon Kao Panom, *Kerr 18832* (A, BM, L, MO); Krasom, Khao Pok, *Haniff & Nur 3638* (SING); Pang-nga, Tap-put, *Kerr 18361* (BM, K, L); Ranong, Kaw Payam, *Kerr 16639* (A, BM, K, L); Trang, Chawng, *Kerr 15154* (BM); Trang, Kaokao, *Rabil 291* (A, BM), *Vanpruk 681* (K); Trang, Sikao, *Kerr 19027* (BM); Tungka, *Curtis 2915* (CAL, SING); Trang, in open jungle, on hilly ground, *Kunstler 1400* (CAL); precise locality unknown, *Curtis s. n.* (SING). SURAT: Langsuan, Tako, *Put 1616* (BM, K); Pato, *Kerr 12208* (BM, K, L, SING); Surat Panom, *Kerr 12414* (BM, K, L).

VIETNAM. Biênhōa, Giarây, *Poilane 185* (F, NY, SAIG); Longthānh, *Thorel s. n.* (A); Trangbom, *Lý van Hôi s. n.* (MO); Trihuyên, *Pierre 4401* (A, NY, P). Dàlat, *Squires s. n.* (NY); Phan thiet, *Dong phuc Long 1404* (SAIG), *s. n.* (SAIG); Phan rang: Cà ná, *Poilane 5955* (SAIG), *8856* (SAIG); Nhatrang, *Poilane 5211* (SAIG), *6770* (SAIG).

This species shows great variability in the shape of the calyx and corolla lobes. In the southern range the calyx lobes are narrowly ovate and acuminate, the corolla lobes narrowly ovate to ovate and slenderly acuminate; the population in the center, which has been treated by many authors as a distinct species (*W. cambodiensis*), has ovate calyx lobes with the apex acute and the corolla lobes ovate to broadly ovate and acute. However these variants intergrade and for this reason, I believe that they cannot be recognized even as subspecies.

EXCLUDED SPECIES

Wrightia afzelii K. Sch. in Engl. Bot. Jahrb. **23**: 231. 1897. = PLEIOCERAS AFZELII (K. Sch.) Stapf Dyer, Fl. Trop. Afr. **4**(1): 166. 1904.

Wrightia baccelliana F. Muell. in Vict. Natural. **8**: 178. 1892. = MELODINUS BACCELLIANUS (F. Muell.) S. T. Blake, Proc. Roy. Soc. Queensl. **59**: 161. 1948.

Wrightia coalita Buch.-Ham. ex Pritz., Ic. Ind. **1**: 1175. 1855. = PERIPLOCA sp. fide Ind. Kew.

Wrightia coccinea, Soland. ex Naudl., Ann. Sc. Nat. Bot., Sér. **3**(18): 126. 1852. = MERIANIA LEUCANTHA Sw., Fl. Ind. Occ. **2**: 826. 1800.

Wrightia cunninghamii Benth., Fl. Austral. **4**: 317. 1869. This is rather an asclepiad according to my observation of the type specimen from the National Herbarium of New South Wales.

Wrightia madagascarensis Boj. ex A. DC. in DC., Prodr. **8**: 408. 1844. = an asclepiad fide A. DC.

Wrightia ottolanderi Koord., Ind. Kew. Suppl. **5:** 275. 1921. = WIGHTIA OTTOLANDERI Koord., Excursionsfl. Java **3:** 172. 1912.

Wrightia parviflora Stapf, Kew Bull. **1894:** 124. 1894. = PLEIOCERAS BARTERI Baill., Bull. Soc. Linn. Paris. **1:** 759. 1888.

Wrightia piscidia G. Don, Gen. Syst. Gard. Bot. **4:** 86. 1838. = MELODINUS MONOGYNUS Roxb., Fl. Ind. ed. Carey & Wall. **2:** 56. 1824.

Wrightia stuhlmannii K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. **4**(2): 183. 1895 = ALAFIA LUCIDA Stapf, Kew Bull. **1894:** 122. 1894.

ENUMERATION OF THE SPECIES

SECTION 1. WRIGHTIA

1. *laevis* Hook. f.
   1a. ssp. *laevis*
   1b. ssp. *millgar* (F. Muell.) P.t.Ngan
   1c. ssp. *novoguineensis* P.t.Ngan
2. *viridiflora* Kerr
3. *flavido-rosea* Trimen
4. *indica* P.t.Ngan
5. *tinctoria* R. Br.
   5a. ssp. *tinctoria*
   5b. ssp. *rothii* (G. Don) P.t.Ngan
6. *kwangtungensis* Tsiang
7. *puberula* (Thw.) P.t.Ngan
8. *sikkimensis* Gamble
9. *tomentosa* R. & S.
   9a. ssp. *tomentosa*
   9b. ssp. *pauciflora* P.t.Ngan
10. *pubescens* R. Br.
    10a. ssp. *pubescens*
    10b. ssp. *candollei* (Vidal) P.t.Ngan
    10c. ssp. *novobritannica* P.t.Ngan
    10d. ssp. *penicillata* (Bailey) P.t.Ngan
    10e. ssp. *laniti* (Blco.) P.t.Ngan
11. *annamensis* Eberh. & Duby
12. *lanceolata* Kerr
13. *angustifolia* Thwaites
14. *lecomtei* Pitard
15. *religiosa* (Teijsm. & Binn.) Benth.

SECTION 2. BALFOURIA

16. *natalensis* Stapf
17. *demartiniana* Chiov.
18. *saligna* (R. Br.) F. Muell. ex Benth.

SECTION 3. WALLIDA

19. *antidysenterica* (L.) R. Br.

SECTION 4. SCLERANTHERA

20. *hanleyi* Elmer
21. *collettii* P.t.Ngan
22. *coccinea* (Roxb.) Sims
23. *dubia* (Sims) Spreng.

NEW OR CRITICAL MALVACEAE FROM CENTRAL AMERICA

By André Robyns

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The revision of the genus *Hibiscus* L. and related genera for the Flora of Panama permits me to describe two new species of *Hibiscus* from Panama: *H. Woodsonii* and *H. cocleanus*. In the past, all the herbarium exsiccatae of *H. Woodsonii* were referred to the genus *Wercklea* and determined as *W. lutea* Rolfe, a species described from Costa Rica. The genus *Wercklea,* which consists of only two species, *W. insignis* Pittier & Standley (Costa Rica) and *W. lutea,* was described by Standley and Pittier in 1916 (Contr. U. S. Nat. Herb. **18:** 112). The generic characters pointed out by the authors as distinctive—3-lobed involucre, comparatively few stamens, oblong anthers, amphitropous ovules and winged capsules—do not, however, satisfactorily distinguish this taxon and consequently I consider *Wercklea* as a synonym of *Hibiscus*. In transferring both species of *Wercklea* to *Hibiscus,* I must give two new names to the latter, as earlier homonyms exist: *H. Wercklei (W. insignis)* and *H. Rolfeanus (W. lutea)*. It is also the purpose of this paper to give a more accurate description of these species.

I wish to express my sincere thanks and appreciation to the directors and curators of the following herbaria for the facilities for study and/or for the loan of material: Chicago Natural History Museum (F), Royal Botanic Gardens, Kew (K), U. S. National Herbarium, Washington, D. C. (US) and School of Forestry, Yale University, New Haven (Y).

Hibiscus cocleanus A. Robyns, sp. nov.; ab affini *H. Woodsonii* A. Robyns pedicello longissimo et 26-30 cm. longo, calyculo usque ad medium 7-lobato deciduoque, calycis basi calyculi cicatrice conspicuo praedito, calyce majore et 4.5-5.5 cm. longo, petalis roseo-rubris tuboque stamineo praecipue parte inferiore piloso primo visu sat differt.

Frutex circa 8 m. altus, ramulis stellato-villoso-arachnoideis. *Folia* alterna, longissime petiolata petioloque tereti prope basim constricto 15-20 cm. longo plus minusve dense stellato-villoso-arachnoideo, stipulis late triangularibus obtusis circa 12 mm. longis et 16 mm. latis utrinque stellato-velutinis et deciduis; lamina subcircularis, basi cordata, apice plus minusve acuta, margine irregulariter dentata, circa 21-24 cm. longa et lata, crasse chartacea, discolor, 9-palmatinervis, supra scabra, sparse stellato-puberula et secundum praecipuos prominentesque nervos stellato-tomentella, infra pallidior, molliter stellato-velutina, praecipuis nervis valde prominentibus nervisque lateralibus reticulatis et prominentibus. *Flores* axillares, solitarii, longissime pedicellati pedicelloque tereti apud basim basive constricto 26-30 cm. longo plus minusve dense stellato-villoso-arachnoideo; calyculus cupuli-

[1] This paper reports results obtained in an investigation supported by National Science Foundation Grant GB-170.

formi-campanulatus, usque ad medium 7-lobatus, circa 2.5 cm. longus, dense stellato-velutinus, deciduus, lobis ovatis acutisque; calyx campanulatus, basi calyculi cicatrice conspicuo praeditus, manifeste 15-20-nervatus, 5-lobatus, 4.5-5.5 cm. longus, extus dense stellato-velutinus et sparsim hispidulus pilisque longis simplicibus vel bifurcatis trifurcatisve, lobis ovato-triangularibus acuminatis 2.5-3 cm. longis et basi circa 1.7 cm. latis manifesteque 3-nervatis; petala 5, anguste obovata, basi attenuata, apice rotundata, circa 12 cm. longa et 4 cm. lata, membranacea, roseo-rubra, extus praecipue parte superiore stellato-villosa, intus fere glabra; androecium circa 10 cm. longum; tubus stamineus versus basim sensim dilatatus, praecipue parte inferiore pilosus, parte superiore glaber, quinto superiore antheriferus, filamentis 5-6 mm. longis, antheris inaequilateraliter hippocrepiformibus; ovarium ovoideum, 5-angulatum, circa 12 mm. longum et 7-8 mm. latum, dense appresso-sericeum; stylus filiformis, tubo stamineo leviter longior, glaber et 5-lobulatus; stigmata 5, capitata denseque fimbrillata. *Capsula* ignota.

PANAMA: COCLÉ: El Valle, July 1962, *J. D. Dwyer 1918* (f., fl.; holotypus MO).

Hibiscus Rolfeanus A. Robyns, nom. nov.; ab affini *H. Wercklei* A. Robyns calyculo 2-3 cm. longo 2(-3)-lobato deciduoque, calyce deciduo, petalis luteis, tubo stamineo circa 8-8.5 cm. longo, filamentis usque ad 3 mm. longis ovarioque dense hispido valde recedit.

Wercklea lutea Rolfe, Kew Bull. 1921: 118. 1921; Standley, Field Mus. Nat. Hist., Bot. Ser. **18:** 677. 1937, 1560. 1938.

Shrub or slender tree, 3-8 m. high, the crown small and round, the bark smooth, the branchlets stellate-pubescent and sometimes sparsely aculeolate. *Leaves* alternate, long-petiolate, the petiole terete, 5-17 cm. long, stellate-tomentose-arachnoid and sometimes sparsely aculeolate, the stipules depressed-ovate-trullate, acute, ca. 1.2 cm. long and 1.7 cm. wide, densely stellate-pubescent, deciduous; blade subcircular, more or less deeply cordate at the base, subacute at the apex, the margins coarsely and obtusely dentate, up to 22 cm. long and 25 cm. wide, discolor, scabrous especially above, stellate-puberulus to sparsely stellate-puberulus above, stellate-tomentose to sparsely stellate-pubescent beneath, the indumentum always much denser when young, usually 7-palminerved, the principal veins prominent especially beneath, the secondary nervation reticulate. *Flowers* axillary, solitary, the pedicel terete, 5-18 cm. long, densely stellate-arachnoid, the hairs sometimes intermixed with short to elongate tubercles topped by 1 or 2 or infrequently even more hyaline setae, the fruiting pedicel up to 19 cm. long, much thickened and up to 7 mm. in diam.; epicalyx 2-3 cm. long, 2(-3)-lobed nearly to the base, deciduous, the lobes broadly ovate, concave, subacute at the apex, appressed-stellate-pubescent; calyx tubular-campanulate, 5-lobed, 4-5 cm. long, densely stellate-hispid and with the hairs sometimes intermixed with pustular-based hyaline setae outside, stellate-velutinous inside, deciduous, the lobes triangular-ovate, subobtuse, 1.5-2.2 cm. long, prominently 3-nerved; petals 5, spatulate-obovate or narrowly spatulate-obovate, rounded at the apex, 10.5-13 cm. long and ca. 4.5 cm. (?) wide, yellow,

membranous, sparsely stellate-arachnoid-pubescent outside; staminal tube gradually enlarged toward the base, about 8-8.5 cm. long, glabrous, antheriferous on the upper ¼, the filaments up to 3 mm. long, the anthers inequilaterally hippocrepiform; ovary oblong-conical, 5-angulate, ca. 9-10 mm. long and 8 mm. in diam. at the base, densely hispid. *Capsule* ellipsoid, prominently 5-angulate, acuminate, (3.5-)6-6.5 cm. long, the acumen ca. 1 cm. long, loculicidally dehiscent into 5 valves, these concave, ca. 3 cm. wide, thick-chartaceous and densely hispid, the hairs pusular-based; seeds reniform, ca. 3.5 mm. long, densely hirsute, the hairs ca. 1.5 mm. long.

Costa Rica: heredia: Yerba Buena, northeast of San Isidro, alt. about 2000 m., wet forest, Febr. 1926, *P. C. Standley & J. Valerio 49705* (f.; US); Cerros de Zurquí, northeast of San Isidro, alt. 2000-2400 m., wet forest, March 1926, *P. C. Standley & J. Valerio 50429* (f.; US). san josé: Las Nubes, on the slopes of Irazú, alt. 7000 ft., Febr. 1920, *C. H. Lankester s. n.* (f., fl., fr.; holotypus K; photo MO); id., alt. about 1500-1800 m., March 1924, *P. C. Standley 38339* (f., fr.; US), along stream, abundant, *P. C. Standley 38645* (f., fr.; US), wet forest, *P. C. Standley 38702* (f.; US); id., May 1924, *Enrique Collado s. n.* (fl.; US); vicinity of Santa Maria de Dota, alt. 1500-1800 m., planted in finca, said to be native of El Naranjo, Dec. 1925—Jan. 1926, *P. C. Standley & J. Valerio 44025* (f., fr.; US).

One of the local names is *burio extranjero* (cf. *P. C. Standley & J. Valerio 44025*).

Hibiscus Wercklei A. Robyns, nom. nov.; affinis *W. Rolfeano* A. Robyns, sed calyculo 1.2-1.5 cm. longo 3(-4)-lobato persistentique, calyce accrescenti, petalis roseis, tubo stamineo breviore et 3.6-4 cm. longo, filamentis brevissimis et ca. 1-1.5 mm. longis ovarioque dense papillato valde distinguendus.

Wercklea insignis Pittier & Standley, Contr. U. S. Nat. Herb. **18:** 112. 1916; Standley, Field Mus. Nat. Hist., Bot. Ser. **18:** 677. 1937, 1559. 1938.

Tree 6-20 m. tall, the trunk 30-50 cm. in diam., the crown lax and rounded. *Leaves* alternate, long-petiolate, the petiole terete, often curved, 5-32 cm. long, glabrous or sparsely appressed-stellate-pubescent, the indument denser when young, the stipules depressed-ovate, ca. 4.5 mm. long and 11 mm. wide, sparsely appressed-stellate-pubescent; blade more or less circular or reniform-circular, more or less deeply cordate at the base, the margins entire or repand-sinuate or coarsely undulate-dentate, 9-33 cm. long and 11-36 cm. wide, slightly discolor, glabrous or nearly so above, sparsely stellate-pubescent beneath, the indumentum denser when young, 7- to 9-palminerved, the principal veins prominent above and very prominent beneath, the secondary nervation reticulate. *Flowers* axillary, solitary or sometimes paired, the pedicel rather slender, terete, 3-6 cm. long, stellate-pubescent or sometimes densely stellate-pubescent, the fruiting pedicel much thickened and much longer, up to 13-18 cm. long and glabrous; epicalyx 1.2-1.5 cm. long, 3(-4)-lobed, the sinuses often extending nearly to the base, the lobes obtuse or rounded, sometimes 2-lobulate, sparsely stellate-pubescent, persistent and becoming glabrescent; calyx narrowly campanulate, 5-lobed, 3-4 cm. long, reddish (according to *Standley 37590*), sparsely stellate-pubescent outside, pubescent-arachnoid inside especially along the margins,

the lobes triangular, acute, 1.6-2.5 cm. long, 3-nerved, the fruiting calyx much accrescent, up to 7 cm. long, membranous and glabrous; petals 5, narrowly spatulate-obovate, connate basally with the staminal tube for about 1 cm., rounded at the apex, 9-13 cm. long and 3.5-5.5 cm. wide, lilac-rose or pink, membranous, sparsely stellate-arachnoid-pubescent outside; staminal tube gradually enlarged toward the base, 5-undulate-lobulate at the apex, 3.6-4 cm. long, glabrous, antheriferous on the upper 1.6-1.8 cm., the filaments very short, ca. 1-1.5 mm. long, the anthers inequilaterally hippocrepiform; ovary oblong-conical, 5-angulate, ca. 5 mm. long and in diam. at the base, densely papillate, the style 3.5-3.7 cm. long, 5-branched, the branches ca. 1.5-2 mm. long, the stigmas densely fimbrillate. *Capsule* oblong-obovoid, prominently 5-angulate, acuminate, 4.5-7 cm. long and 2-2.5 cm. in diam., the acumen 1-1.3 cm. long, loculicidally dehiscent into 5 concave, thick-chartaceous valves, these densely hispid, the hairs pustular-based; seeds reniform, ca. 2.3-3 mm. long, densely lanate or hirsute, the hairs ca. 2.5-3 mm. long.

COSTA RICA: ALAJUELA: La Peña de Zarcero, alt. 4200 ft., cloud forest area, Dec. 1937, *Austin Smith A708* (f., fl.; F). HEREDIA: near La Paz waterfall, near Cinchona, north slope of Volcán Poás, alt. 1600 m., April 1956, *L. O. Williams 20317* (f., fl.; F). PUNTARENAS: Pejivalle, riverside, July 1924, *C. H. Lankester 878* (f., fl., fr.; US). SAN JOSÉ: San José, Sr. Jiménez' Garden, 1918, *W. W. & H. E. Rowlee 286* (f., fl., fr.; US); suburb of San José, cultivated, Aug. 1920, *W. W. Rowlee & H. E. Stork 968* (f., fl., fr.; US); Guadelupe, cultivada en un jardín, Oct. 1910, *O. Jiménez 19* (f., fl.; US); id., cult., 1916, *O. Jiménez, s. n.* (f., fr.; US); id., garden, July 1920, *W. Popenoe 1022* (*Seed & Plant Introduction 51125*) (f., fl.; US); id., cult., alt. about 1150 m., *P. C. Standley 33339* (fr; US); La Palma, forests, alt. ca. 1460 m., *C. Wercklé s. n.* (f., fl., fr.; holotypus US *678449;* isotypi US *678448 &* US *678451*); id., forests, alt. 1459 m., Sept. 1898, *A. Tonduz s. n.* (*Herb. Inst. Phys.-Georgr. Nat. Costaricensis 12536*) (f., fl., fr.; US); id., Aug. 1918, *W. W. & H. E. Rowlee 254* (f.; US); id., *A. M. Brenes 3739* (f., fl.; F); id., forests, alt. 1250-1275 m., Nov. 1925, *A. M. Brenes 4598* (f., fl.; F); Cascajal, June 1919, *C. H. Lankester 329* (f., fl., fr.; K, US); La Hondura, alt. 1300-1700 m., along stream, common, sometimes forming pure stands, March 1924, *P. C. Standley 37590* (f.; US); id., alt. 1300 m., Aug. 1933, *M. Valerio 753* (f., fl.; F).

Hibiscus Woodsonii A. Robyns, sp. nov.; *H. Rolfeano* A. Robyns affinis, sed calyculo 6-10-lobato persistentique, calyce breviore 2.8-3.8 cm. longo persistentique primo visu valde differt; etiam *H. cocleano* A. Robyns proximus, sed pedicello breviore et 5-16 cm. longo, calyculo plus minusve usque ad basim lobato persistentique, calyce breviore persistentique, petalis luteis tuboque stamineo glabro primo visu sat recedit.—Fig. 1.

Wercklea lutea Auct. non Rolfe; Standley, Ann. Missouri Bot. Gard. **27:** 319. 1940; Brizicky, Stern & Chambers, Trop. Woods **109:** 72. 1958.

Arbor 10-20 m. alta, trunco 30-35 cm. diam., ramulis stellato-villoso-arachnoideis, ligno molli. *Folia* alterna, longe petiolata petioloque tereti basi saepe constricto usque ad 19 cm. longo stellato-tomentello ad stellato-puberulo, stipulis late ovatis subacutis usque ad 2.5 cm. longis et 2 cm. latis stellato-velutinis; lamina subcircularis circularisve, interdum plus minusve subangulata, basi cordata, margine irregulariter crasseque dentata, usque ad 28 cm. longa et lata, discolor, utrinque stellato-puberula, statu juvenili indumento densiore, 7-9-palmatinervis,

praecipuis nervis praecipue infra prominentibus, nervis lateralibus reticulatis. *Flores* axillares, solitarii, pedicello tereti interdum basi constricto 5-16 cm. longo stellato-tomentello ad stellato-puberulo, pedicello fructifero valde crassiore; calyculus 1.7-2.2. cm. longus, plus minusve usque ad basim 6-10-lobatus lobisque ovatis acutis marginibus extus recurvatis usque ad 1 cm. latis utrinque stellato-tomentellis

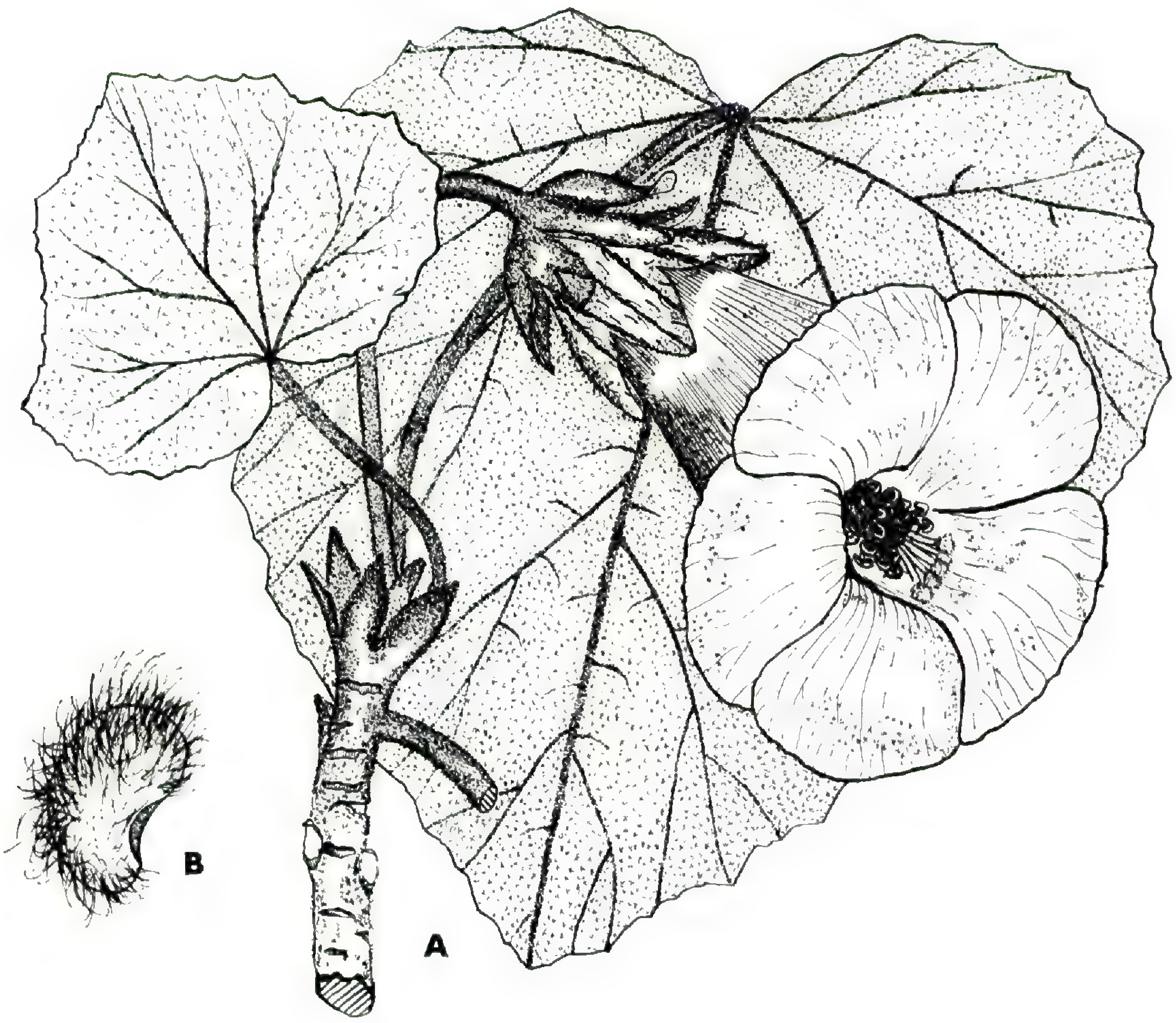

Fig. 1. Hibiscus Woodsonii A. Robyns: A, flowering branch (× ½); B, seed (× 5). After *G. White 41.*

ad stellato-puberulis, persistens; calyx campanulatus, plus minusve usque ad medium 5-lobatus, 2.8-3.8 cm. longus, manifeste 15-nervatus, extus stellato-tomentellus vel stellato-puberulus et sparsim setiferus setisque longis simplicibus vel rare bifurcatis basi pustulosis, intus parte superiore minute arachnoideo-villosulus, persistens vel interdum leviter accrescens, lobis triangularibus acutis 1.3-1.7 cm. longis manifesteque 3-nervatis; petala 5, obovata, basi cuneato-unguiculata, apice rotundata, 8-12.5 cm. longa et 5-6 cm. lata, pallide lutea, membranacea, parte superiore sparse stellato-pubescenti ad glabrescenti; tubus stamineus cylindraceus, versus basim sensim dilatatus, apice 5-undulato-lobulatus, circa 7 cm. longus, glaber, ⅕ superiore antheriferus, filamentis circa 6 mm. longis, antheris inaequilateraliter hippocrepiformibus et circa 2 mm. longis; ovarium oblongo-conicum, prominenter 5-angulato-alatum, circa 8 mm. longum et 7 mm. diam., pilis rudimentariis obtectum; stylus filiformis, tubo stamineo longior, apice 5-divisus lobisque 2-3 mm. longis, glaber; stigmata capitata denseque fimbrillata. *Capsula* ellipsoidea, promi-

nenter 5-angulata, longe acuminata, 5-6.5 cm. longa, acumine circa 1-1.5. cm. longo, in valvis 5 concavis 2-2.7 cm. latis sublignosis dense hispidis pilisque basi pustulosis loculicida; semina reniformia, circa 3-4 mm. longa, villosa.

PANAMA: CHIRIQUÍ: valley of upper Río Chiriquí Viejo, vicinity of Monte Lirio, March 1938, *G. White 41* (f., fl., fr.; MO); id., near El Volcán, July 1938, *P. White 175* (f., fl.; F, MO); slopes of Volcán Barú near Cerro Punta, alt. 6000 ft., June 1957, *Stern & Chambers 77A* (f., fl., j.; Y); vicinity of Bajo Chorro, alt. 1900 m., July 1940, *Woodson & Schery 604* (f., fl.; holotypus US, isotypus MO); Palo Alto, just east of Boquete, elev. 5000 ft., partly disturbed forest of cloud-forest type, July 1959, *Stern, Chambers, Dwyer, Ebinger 1087* (f., fl.; MO, US).

A common name is *mompala amarilla* or *amapala amarilla,* and the bast is used for making rope (cf. *G. White 41*); the flowers are reported to have a very fragrant perfume (cf. *P. White 175*).

The specific epithet honors the late Dr. Robert E. Woodson, Jr.

CYTOPALYNOLOGICAL STUDY OF AFRICAN HEDYOTIDEAE (RUBIACEAE)[1]

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In the Americas only five or six genera are known in the rubiaceous tribe *Hedyotideae* (Lewis 1962a, 1965), but in Africa, south of the Sahara and in adjacent islands, at least thirty are found. A cytopalynological study of these genera was undertaken in an attempt to describe their chromosomal complements and pollen forms in the tribe's center of diversity and to compare them with those from the Americas. Such a study should better characterize the tribe in these continents and should develop an understanding of major phylogentic trends in the whole tribe *Hedyotideae*. Evidence from these disciplines might also improve present classifications by confirming or rejecting certain intergeneric realignments which in the past have been proposed for African members of the tribe.

The genera are discussed under four groupings, three with known chromosome numbers, and the fourth unknown. Procedures, materials and results of the chromosomal study are summarized in Appendix 1. Species studied palynologically, together with the techniques involved, are given in Appendix 2. Author citations for species and lower taxa are given in the appendices when these have been studied cytopalynologically.

I. BASIC CHROMOSOME NUMBER X = 9.

Agathisanthemum Klotzsch

An African genus consisting of six species of which three are restricted in distribution, *Agathisanthemum* is said by Bremekamp (1952) to show a close relationship with the Asian section *Diplophragma* W. & A. of *Hedyotis* L., particularly in its form of capsular dehiscence. Among the African members of the *Hedyotideae* he suggested a close affinity with *Dibrachionostylus*.

The chromosomes of *A. bojeri* and *A. globosum* are small and based on $x = 9$ and resemble those of *Oldenlandia* and a number of allied genera.[2] Both subspecies[3] of *A. bojeri* are diploid ($n = 9$) and *A. globosum* is tetraploid ($n = 18$).

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[1]A portion of this study was completed at the Royal Botanic Gardens, Kew, during the tenure of a John S. Guggenheim Memorial Foundation Fellowship (1963-64). To the director of the Foundation for this award and to the director and staff at Kew for the many facilities placed at my disposal, I am most grateful. The study was also supported by Grant No. G-21818 from the National Science Foundation.

[2] Whenever it is suggested that taxa are related or allied, it means that they are morphologically similar over a large range of structures (often including palynological and chromosomal); nevertheless the relationship remains hypothetical.

[3] On discussing the use of subspecies as an infraspecific category, particularly in answer to remarks by van Steenis (Flora Malesiana, ser. 1, **5:** 167-234. 1957), Bremekamp (Proc. K. Ned. Akad. Wetensch., ser. c, **62:** 107. 1959) noted that he had only once used the category and this in the genus *Acanthus*. Clearly, however, the subspecies he described for *A. bojeri* (1952) are a second exception.

Ann. Missouri Bot. Gard. **52**(2): 182-211. 1965.

The pollen of *A. bojeri*, *A. globosum* and *A. quadricostatum* is colpororate with apertures consisting of long, narrow colpi and compound ora (cf. Lewis, 1965). These ora consist of an os, designated type A, which is delimited by a very thin layer of nexine in the equatorial zone and surrounded by a much thickened layer of nexine, and a second os, designated type B, which is pore-like and surrounded by a distinct nexinous margin. The type A os is usually in the shape of an elongated diamond, whereas the type B os is circular and ca. 2.7 μ in diameter (Fig. 16f). The grains are 3- to 4-aperturate, subspheroidal and vary in size from only 20 μ (E) × 19.3 μ (P) for the long-styled flowers of *A. bojeri* to 29.3 μ × 26.7 μ for the short-styled flowers of *A. quadricostatum*. Pollen of short-styled flowers of *A. bojeri* is slightly larger (21.3 μ × 22.7 μ) than that of long-styled ones, but pollen from both floral types of *A. bojeri* (2*x*) is smaller than the pollen from the isostylous, tetraploid species *A. globosum* (26.9 μ × 26.7 μ). The sexine of all species is thin (ca. 1-1.4 μ) and finely reticulated.

The aperture morphology for *Agathisanthemum* is the same as that known for the monotypic genus *Lelya*, but such a specialized aperture has been described for a majority of the North American species of *Hedyotis* subg. *Edrisia* (Lewis, 1965). This kind of aperture is not found in the Asian members of *Hedyotis* thought to be closely allied to *Agathisanthemum* nor in *Dibrachionostylus*.

Amphiasma Bremek.

A genus erected by Bremekamp (1952) to include those species formerly recognized under *Oldenlandia* having few, dorsiventrally flattened seeds and cylindrical stipular sheaths, *Amphiasma* consists of eight species endemic to Africa. All are restricted in distribution and none is well collected. Bremekamp noted that *Amphiasma* is most nearly allied to *Eionitis*, *Lelya* and *Oldenlandia*.

The chromosomes of *Amphiasma* are small and based on $x = 9$. An undetermined species from South West Africa is diploid and *A. merenskyanum* is tetraploid.

The pollen of *A. benguillense* and *A. merenskyanum* is small (26.7 μ × 20 μ and 25.3 μ × 24 μ, respectively), subspheroidal, 3-colporate with long, narrow colpi and simple, type A ora distinctly diamond-shaped (Fig. 16b), and with a thin sexine (ca. 1.2 μ in thickness) having fine or medium-fine reticulations. This is indistinguishable from the pollen of the majority of *Oldenlandia* species in the structure of the aperture, in pollen size and shape, and in the characteristics of the wall.

Conostomium Cuf.

Nine species of *Conostomium*, all endemic to Africa, are recognized under three subgenera. Bremekamp (1952) distinguished the genus from its nearest allies (*Oldenlandia, Kohautia, Pentanopsis*) by the long cylindrical corolla tube with included anthers and typically exserted styles, large fruit and granulated basal walls of the testa. Emphasizing the distinctiveness of the pollen grains he describes them as ". . . larger than in the other genera belonging to this circle of affinity, they

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possess a very thin wall, and they are not colporate but porate. The pores, moreover, are enclosed between a couple of short, easily staining bars, one at the top and the other one at the base of the pore."

The chromosome complements of *C. kenyense* (4*x*) and *C. natalense* (2*x*) are based on $x = 9$ and the chromosomes are small, e.g., metaphase II chromosomes of *C. natalense* average only 1.1 μ in length (Fig. 1). This is comparable to the chromosome sizes for *Kohautia cynanchica* (Fig. 3) and *Oldenlandia capensis* (Fig. 4) at the same stage of meiosis.

Pollen representative of the three subgenera of *Conostomium* is medium in size (29.3 μ × 28 μ for *C. kenyense* to 39.4 μ × 40 μ for *C. quadrangulare*), subspheroidal, 3-colporate, with colpi medium (13 μ) to short (8 μ) in length, narrow to rather broad (3.8 μ) and simple type A ora, 2.7-6.7 μ high, delimited vertically by thick concentrations of nexine which are horizontally incomplete (Fig. 16i, j). The sexine is thin (ca. 1 μ) to thick (ca. 3 μ) with fine to coarse (in *C. natalense*) reticulations, excepting the pollen of *C. quandrangulare* which is verrucose. The nexine is ⅔ the thickness of the sexine, although when adjacent to the ora it is about twice as thick.

Bremekamp (1952) described the pollen from seven species of *Conostomium* as porate, but of the four species examined in this study I was able to measure distinct colpi. The colpi may, however, be short and since Bremekamp apparently observed non-acetolyzed pollen, a brevicolpate condition could easily be overlooked. Bremekamp's description of the pores enclosed by "two bars" does characterize the ora of *C. natalense* (subg. *Conostomium*) and *C. quadrangulare* (subg. *Hockstetteria*) as illustrated in Fig. 16j. These crescent-shaped nexinous thickenings delimiting the upper and lower limits of each os are unique among the pollen studied. It does not describe the pollen of species in the subg. *Beckia (C. kenyense, C. longitubum)* for which the nexinous thickenings are coarsely triangular-shaped (Fig. 16i). These are not unlike those for the species of group 1 in *Hedyotis* subg. *Edrisia* (Lewis, 1965) and for some species of African *Oldenlandia* (Fig. 16c).

According to Bremekamp (1952), the pollen for *Conostomium* is larger than that of other genera belonging to this "circle of affinity." The mean size for three of the species I examined was 29.5 μ × 29.3 μ with the pollen of *C. quadrangulare* considerably larger (39.3 μ × 40 μ). Bremekamp's diagram (1952 : 295) of the pollen of *C. longitubum* measures less than 20 μ in diameter, even though his size

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Fig. 1-15. Chromosomes drawn with the aid of a camera lucida originally at × 2800, reduced by ca. ¼ in reproduction. Fig. 1. *Conostomium natalense, Lewis 6332, n* = 9 (1 set metaphase II). Fig. 2. *Kohautia grandiflora, Lewis 5997, n* = 9. Fig. 3. *K. cynanchica, Lewis 6313, n* = 9 (1 set metaphase II). Fig. 4. *Oldenlandia capensis, Lewis 6210, n* = 9 (1 set metaphase II). Fig. 5. *O. cephalotes, Lewis 6314, n* = 9. Fig. 6. *O duemmeri, Lewis 6018, n* = 9. Fig. 7. *O. echinulosa, Lewis 6091, 2n* = 18. Fig. 8. *O. herbacea* var. *goetzii, Lewis 6228, n* = 9. Fig. 9. *O. saxifrigoides, Hemming 1673, 2n* = 18. Fig. 10. *Pentodon pentandrus, Lewis 6027, n* = 9. Fig. 11. *Otomeria elatior, Lewis 6215, n* = 10. Fig. 12. *Pentas longiflora, Lewis 5962, n* = 10. Fig. 13. *P. zanzibarica* var. *intermedia, Lewis 6005, n* = 10. Fig. 14. *Manostachya staelioides, Lewis 6128, 2n* = 44. Fig. 15. *Pentanisia ouranogyne, Lewis 5965, n* = 20.

descriptions for seven species average 23.3 μ to 25 μ. Providing that *Oldenlandia* is considered a genus belonging to this circle of affinity, then his measurements of pollen are very similar to a majority of *Oldenlandia* species and even the larger sizes recorded in this study from acetolyzed grains are also known for *O. herbacea*, *O. monanthos*, *O. rupicola* and others. They are also similar in size to the grains of *Pentanopsis fragrans* Rendle, but larger than those for all species of *Kohautia* studied.

Finally, Bremekamp (1952) described the pollen of *Conostomium* as very thin-walled and although such a sexine is typical of members of the subg. *Beckia*, all species in the other subgenera are thick-walled, as thick as any known for African members of the *Hedyotideae*.

Although the distinctiveness of the pollen for *Conostomium* has been incorrectly overemphasized, it does illustrate several unique features, the most striking of which is the brevicolpate condition characteristic of species in the subgenera *Conostomium* and *Hochstetteria*. These species also have pollen with unusual crescent-shaped nexinous thickenings partially surrounding their ora. Moreover, the verricose sexine known for *C. quadrangulare* is unique among the pollen of members of this tribe in Africa.

Dibrachionostylus Bremek.

The monotypic genus *Dibrachionostylus* was separated from *Oldenlandia* largely on the basis of capsule dehiscence, viz., both loculicidally and septicidally for the former and only loculicidally for the latter. Bremekemp (1952) closely associated *Dibrachionostylus* with *Agathisanthemum* because of their similar dehiscence.

The chromosomes of *D. kaessneri* are small with $n = 9$. The pollen is medium-small (26.7 μ × 24.7 μ), subspheroidal, 3-colporate with long, narrow colpi and type A ora, 4 μ high and indefinite horizontally, with ± thin sexine (ca. 1.5 μ thick) having medium reticulations and with nexine about ½ as thick as the sexine.

In aperture morphology *Dibrachionostylus* differs markedly from the more specialized form known for *Agathisanthemum*, but the aperture is similar to that described for *Amphiasma*, *Oldenlandia* and *Pentodon*.

Kohautia C. & S.

Forty-eight species of *Kohautia* from continental Africa are described (Bremekamp, 1952), with perhaps 12 additional species known to Madagascar and southern Asia. *Kohautia* is distinguished from its closest African allies by a cylindrical corolla tube having a slightly widened upper region containing sessile anthers, while the short-style is usually included in the narrow, lower part of the tube. The monomorphic, short-styled condition is, with the exception of a few individuals of *Conostomium*, unique among the African members of the tribe. The same floral morphology is known for some species of *Hedyotis* subg. *Edrisia* indigenous to the southern United States (Lewis, 1962a). As noted by Bremekamp (1952), pollen grains are 3- to 8-colporate and small and as such differ from the grains known for *Oldenlandia* and other allied African genera.

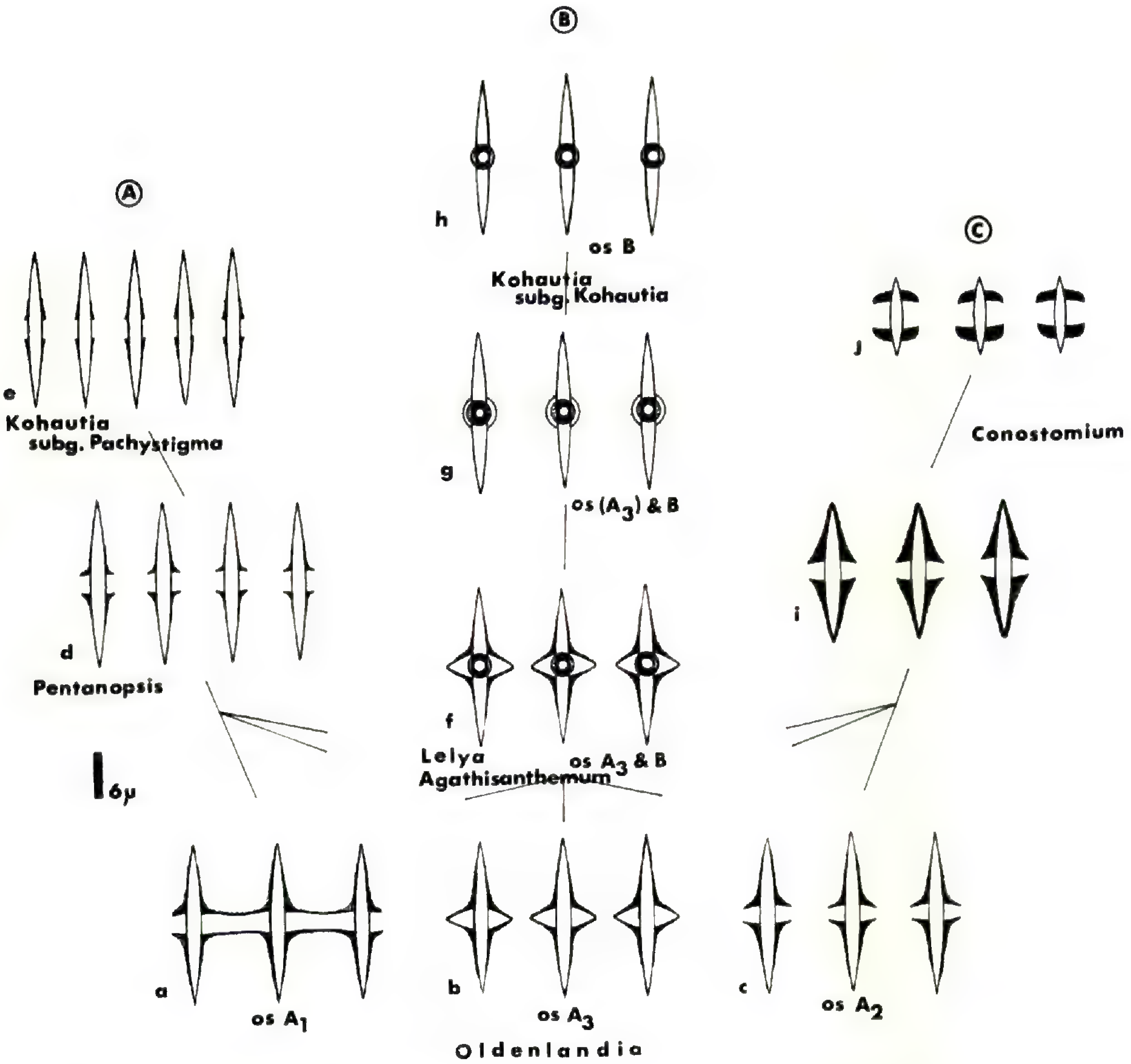

Fig. 16. Diagrammatic representation of pollen aperture types for *Oldenlandia* and its allies in Africa. Three lines of modification lead from a 3-aperturate condition having long colpi and simple, type A ora to: (A) 4- and 5-aperturate types (up to 8, not illustrated) in closer proximity with an associated decrease in nexinous thickenings and a consequent weakening of os A_2; (B) compound ora with distinct oral types A_3 and B, to a very reduced A_3, to its absence and presence only of os B; (C)colpi medium in length and to a brevicolpate condition associated with a nexinous concentration surrounding the os. Fig. a-c - All species of *Oldenlandia* and many *Hedyotideae* illustrating kinds of ora, type A. Fig. d - *Pentanopsis,* some *Kohautia* species. Fig. e - Most species of *Kohautia* subg. *Pachystigma.* Fig. f - *Agathisanthemum, Lelya.* Fig. g - *Nesohedyotis,* some species of *Kohautia* subg. *Kohautia.* Fig. h - Some species of *Kohautia* subg. *Kohautia.* Fig. i - *Conostomium* subg. *Beckia.* Fig. j - *Conostomium* subg. *Conostomium* and subg. *Hochstetteria.*

The chromosome number for *K. senegalensis* C. & S. was reported by Hagerup (1932) from west African collections as $2n = 18$ and for *K. aspera* by Raghaven and Rangaswamy (1941) from India as $n = 18$. To these counts are added those for eight other taxa, as well as a verification of the number for *K. aspera* from an Ethiopian collection. All species have a basic complement of $x = 9$ consisting of either small or medium-small chromosomes. The chromosomes for *K. cynanchica* (Fig. 3) average approximately 1.1 μ long and are similar in size to those illustrated for *Conostomium natalense* (Fig. 1) and *Oldenlandia capensis* (Fig. 4). The bivalents

of *K. grandiflora* each have chromosomes averaging ca. 2 μ in length (Fig. 2) and resemble those of *Oldenlandia duemmeri* (Fig. 6). Diploid and tetraploid species are common, but only *K. virgata* was found to be hexaploid. Infraspecific chromosomal races were not observed, but otherwise the chromosomal pattern for *Kohautia* resembles that known for *Oldenlandia*.

Pollen from 20 species of *Kohautia* was studied which represents slightly more than ⅖ of the described African species. Of the remainder, ⅖ are known from only the type collection or from this and one other specimen. The grains are small (12 μ × 12.8 μ to 22.7 μ × 21.3 μ), subspheroidal, usually prolate or oblate-spheroidal, commonly 3- to 5-, rarely 6- to 8-, aperturate with size correlated with aperture number, viz., smallest grains 3-colporate, those having a polar axis 18 μ or more in diameter always 4- or more colporate. The colpi are long and narrow, occasionally constricted equatorially and with smooth membranes. The ora are simple or infrequently compound.

Pollen of the subg. *Pachystigma* consists of type A ora, either obscure laterally or rarely synclinorate. Pollen of the subg. *Kohautia* possesses type B ora which are usually circular (ca. 1.4 μ), thinly crassimarginate with the margin occasionally surrounded by a hallow-like area of thin nexine, thereby resembling compound ora. The sexine is ca. 1 μ thick, simplibaculate, usually medium to finely reticulated in the subg. *Kohautia* and is usually coarsely reticulated in the subg. *Pachystigma*.

Palynologically the species of *Kohautia* divide into two distinct groups corresponding exactly to a subgeneric classification proposed by Bremekamp (1952) on other evidence. The distinction of aperture types is universal among the species examined. Moreover, different subgeneric tendencies exist for pollen size, aperture number and certain exine features. These are summarzied as follows:

Subg. *Kohautia* (based on 14 species).

(1) simple os, type B, occasionally surounded by an area of thin nexine (compound os).
(2) smaller grains, mean size 16.9 μ × 16.1 μ.
(3) apertures typically 3 or 4, less commonly 5, very rarely 6.
(4) usually thin, finely reticulated sexines.

Subg. *Pachystigma* (based on 6 species).

(1) simple os, type A, obscure horizontally or rarely synclinorate.
(2) larger grains, mean sizes 20.8 μ × 19.9 μ.
(3) apertures typically 4 to 5, infrequently and never exclusively 3, less commonly 6 to 8.
(4) somewhat thicker, coarsely reticulated sexines.

I have noted that some North American species of *Hedyotis* possess a floral morphology similar to that of all described species of *Kohautia*. These American species also have in common with the subg. *Kohautia* a simple, crassimarginate os (type B). This parallelism is striking, for among the pollen of all Afro-American species of the *Hedyotideae* examined, only these two groups have such apertures. The species from the two continents differ by a number of important characters (e.g., seed morphology) so that the taxa are probably only of distant relationship.

The specialized parallelisms in both floral and pollen morphology do, however, suggest a genetic affinity of some significance (cf. Cronquist, 1963).

Pollen apertures of some species of the subg. *Kohautia* possess a vague, nexinous thin area adjacent to the margin of the os. This suggests an intermediate form between the clearly defined nexinous thin region as found in *Agathisanthemum*, *Lelya* and many North American species of *Hedyotis*, and the ± evenly thickened nexine adjacent to the os B of most species of the subg. *Kohautia*. These oral types are illustrated in Fig. 16g, h.

The absence of a crassimarginate os (type B) for all species examined in the subg. *Pachystigma* identifies the pollen of this group. Even the type A os is very obscure ventrally for the nexinous thinnings adjacent to the colpus measure only ca. 0.5 μ in thickness. Horizontally the ora extend for about 1-2 μ on each side of the colpus, but, excepting *K. cuspidata*, these extensions are difficult to observe. For *K. cuspidata* the ora are weakly continuous, but these often fade because of reduced nexinous concentrations away from the colpi. Furthermore, there is an increase in the average number of apertures per grain which brings the apertures closer. These aperture conditions in species of the subg. *Pachystigma* represent a second line of development for the pollen of *Kohautia* (Fig. 16d, e).

With the exception of the monotypic genus *Pentanopsis* all species of *Kohautia* can be readily separated by their pollen from those of *Oldenlandia* and all other African taxa in the tribe *Hedyotideae*.

Lelya Bremek.

The monotypic genus *Lelya* was erected by Bremekamp (1952) for plants having thick, woody-walled, conical beaked capsules which are tardily dehiscent and few seeded.

Among a group of unnamed *Oldenlandia* at the British Museum, I noted the type of *Spermacoce prostrata* R. Good (J. Bot. **65** (suppl. 2): 42. 1927). Good observed that "this species is very unlike any other member of the genus known to me in its general habit, but the structure of the flowers and fruit shows that it is a *Spermacoce*." On dissecting one fruit from the type specimen I found a total of eight angular seeds, not Good's "loculis 1-ovulatis." The fact that the plant is a member of the tribe *Hedyotideae* rather than a member of the *Spermacoceae* had already been recognized by Gilleland, for in this folder was a sheet annotated as an *Oldenlandia* named after the collector Jelf (*Jelf 20*, Fort Roseberry, N. Rhodesia) and signed H. B. G. This new epithet is also pencilled on Good's type, although to my knowledge it remains unpublished. The specimens are, in fact, *Lelya osteocarpa Bremek.*, which must become *Lelya* **prostrata** (R. Good) W. H. Lewis, comb. nov. (*Spermacoce prostrata* R. Good, J. Bot. **65** (suppl. 2): 42. 1927; *Lelya osteocarpa* Bremek., Verh. K. Ned. Akad. Wet., Afd. Natuurk., ser. 2, **48:** 181. 1952). The holotype is from Angola: Cuanza Norte District, near Capijango, near Lucala, *Gossweiler* 7385, 5 Jan. 1918 (BM). Two varieties are recognized: a pubescent form, *L. prostrata* (R. Good) W. H. Lewis var. *prostrata*, and a glabrous form, *L. prostrata* var. **angustifolia** (Bremek.) W. H. Lewis, comb. nov., based on *L.*

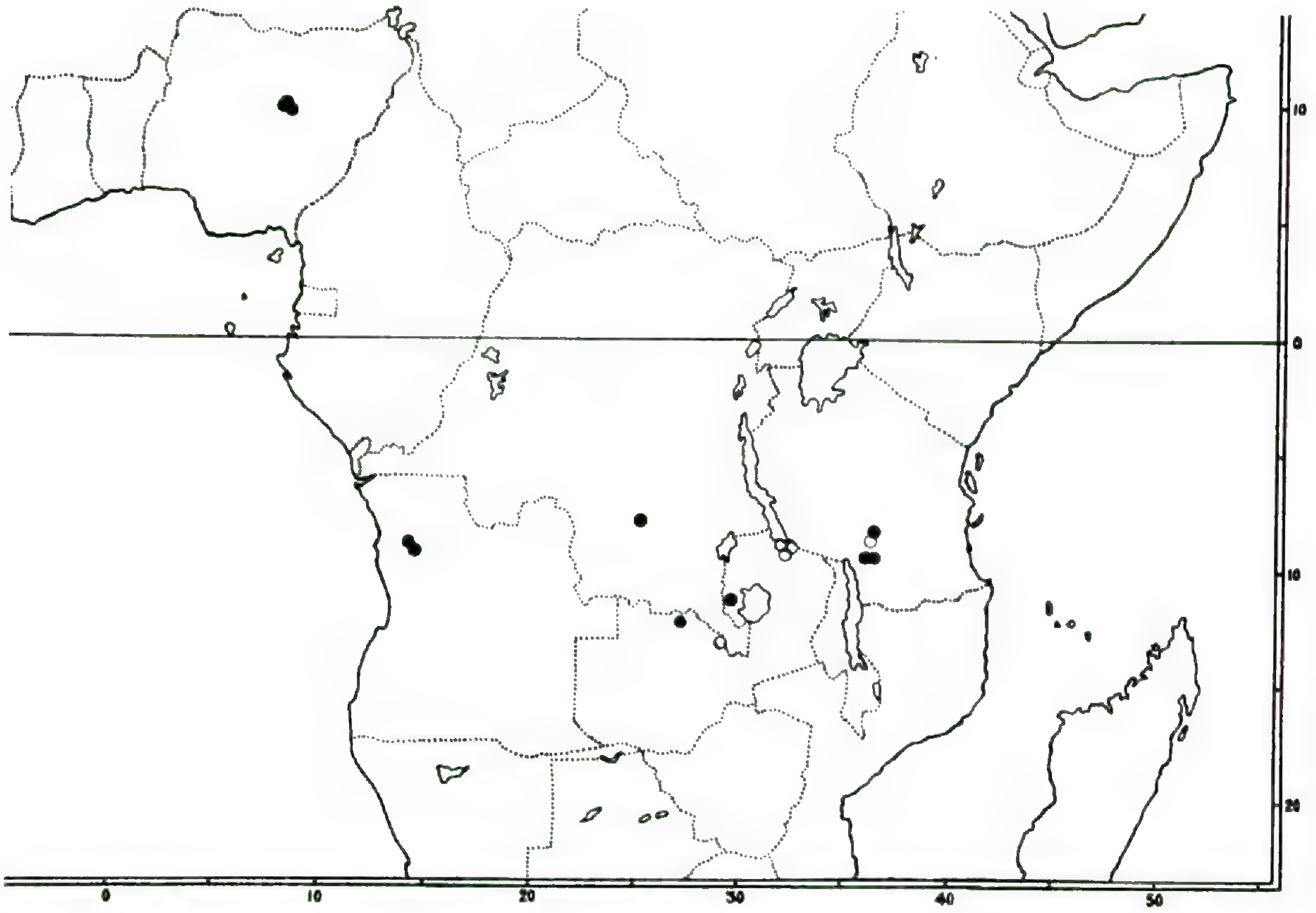

Fig. 17. Distribution of *Lelya prostrata* var. *prostrata* (•) and var. *angustifolia* (○).

osteocarpa var. *angustifolia* Bremek. (Verh. K. Ned. Akad. Wet., Afd. Natuurk., ser. 2, **48:** 183. 1952).

Bremekamp (1952) recorded the genus from the Congo (Léop.), Nigeria, N. Rhodesia and Tanganyika. Additional collections are now reportable from these countries, together with the first records from Angola as given below. The known distribution (Fig. 17) is discontinuous, which may be due to incomplete collecting or the preference of the species for savannahs and plateau around 1,000 m. generally subject to fires or to both.

All individuals on the type sheet of *L. prostrata* var. *angustifolia* are subglabrous and have very narrow leaves. However, the subglabrous plants considered here under var. *angustifolia* rarely have leaves as narrow as those known for the type collection. The stems of plants collected by Fanshawe *(F361)* and Richards *(2049)* are more pubescent than is typical of the var. *angustifolia,* but the leaves, ovaries and corollas are glabrous. This variety is common in northeastern N. Rhodesia while the var. *prostrata* is more prevalent elsewhere.

L. prostrata var. *prostrata* (additional to Bremekamp, 1952). ANGOLA. Cuanza Norte Dist.: near Capijango, near Lucala, *Gossweiler* 7385 (BM, holotype); Lamba Caju, *Gossweiler 8488* (BM). NIGERIA. Plateau Prov.: Heipang, *Keay et al.* FHI 37612 (K); Werran, collector unknown, 27 Apr. 1946 (K). N. RHODESIA. Northern Prov.: Fort Roseberry Dist., Fort Roseberry, *Jelf 20* (BM). TANGANYIKA. Southern Highlands Region: Iringa Area, 4.5 miles N.E. of John's Corner, *Lewis 6067* (K, MO, US).

L. prostrata var. *angustifolia* (additional to Bremekamp, 1952). N. RHODESIA. Northern Prov.: Abercorn Dist., 1 mile S. of Abercorn, *Lewis 6119* (K, MO, US); ca. 5 miles S. of Abercorn, *Greenway & Brenan* 8233 (K); Mpulungu, *Richards 2019, 2049* (K); road to Ningi Pans, *Richards 13161* (K); Lunzua Protected Forest Area, *Lawton 442* (K); Western Prov., Ndola, *Fanshawe F361* (K).

Lelya prostrata is a tetraploid species ($n = 18$) with small chromosomes. The pollen is medium small (26.6 μ × 24 μ), subspheroidal, 3- to 4-aperturate with long, narrow, equatorially constricted colpi and compound ora consisting of type A ora, either diamond-shaped or occasionally ± synclinorate to ca. 3 μ high, and type B ora which are small (2 μ), circular or lolongate, and surrounded by a thin margin which is less than 1 μ in thickness. The sexine is about 2 μ thick, medium to finely reticulated and the nexine is ⅔ as thick as the sexine.

The same kind of aperture has been found for *Agathisanthemum* and for some North American species of *Hedyotis* except that the type B os for *Lelya* is much more delicate (Fig. 16f). Like *Agathisanthemum*, the apertures may also number more than three per grain. By having compound ora, the pollen of *L. prostrata* differs from all known species of *Oldenlandia;* for the latter, ora are invariably simple.

Oldenlandia L.

The pantropical genus *Oldenlandia* is common throughout Africa south of the Sahara where 61 species have been reported (Bremekamp, 1952). A number of these are poorly known and some are of questionable validity (cf. Hepper, 1963; Lewis, 1964) but, regardless of these, the genus in Africa is represented by more species than in all other tropical areas combined. Africa is certainly the center of morphological diversity for the genus and there is strong evidence that the dispersal of the most widespread (and type) species, *O. corymbosa* L., was from central-east Africa with migration in two directions: first to southern Asia and the western Pacific, and then to western Africa and the Americas (Lewis, 1964). This example might also be indicative of the origin and pathways of migration for the genus as a whole.

Chromosome numbers for 23 species, representing 10 of the 16 described subgenera, are listed in Appendix 1. Excepting the counts for four species, all are new reports for *Oldenlandia*. Of the four, the number for *O. lancifolia* ($n = 18$) verifies that recorded by Lewis (1962b) from Mexican material, the tetraploid count ($n = 18$) for *O. capensis* confirms the reported number of Hagerup (1932) from a west African collection and the count from Indian material for *O. pumila* (as *O. crystallina* Roxb.) ($n = 9$) by Raghaven and Rangaswamy (1941) is verified by counts for material originating from Hyderabad and Uganda. The diploid, tetraploid and hexaploid numbers obtained for *O. corymbosa* are discussed in detail elsewere (Lewis, 1964).

The basic chromosome number for all species of *Oldenlandia* s. s. examined is $x = 9$. In Africa the frequency of diploid species is 48% of this total. Tetraploids account for 26%, whereas 26% of the species were found to have more than one euploid race. These results are summarized in Table 1 together with the known data for related species in *Hedyotis* (Lewis, 1962a; Lewis & Terrell, 1962). For species in the latter genus, infraspecific euploidy totals 28%, almost identical in frequency and kind as in the African species of *Oldenlandia*. Inter- and infraspecific aneuploidy, currently unknown for the African species, is also widespread for the American species. It appears that numerical chromosomal changes are im-

Table 1. Frequency of euploidy and aneuploidy in African *Oldenlandia* and North American *Hedyotis* subg. *Edrisia*.

Chromosomal composition of species		Frequency (%)	
		Africa (23 spp.)	N. Am. (25 spp.)
Diploid		48	64
Tetraploid		26	8
Diploid and tetraploid		17.5	20
Diploid and 2 polyploid races		8.5	4
Tetraploid and hexaploid		0	4
Total infraspecific euploidy		26	28
Basic aneuploid series:	$x = 6$	0	16
	$x = 7$	0	8
	$x = 8$	0	16
	$x = 9$	100	4
	$x = 11$	0	36
	$x = 13$	0	20
Infraspecific aneuploidy		0	8
Species with 1 chromosomal race		74	64
Species with 2 or more races (euploid and aneuploid)		26	36

portant factors in the evolution of the species known for each group, by euploidy in both, but by aneuploidy only among the North American species.

The mitotic chromosomes of O. *echinulosa* measure ca. 1.1 μ in length (Fig. 7) and those of O. *saxifrigoides* ca. 1.1-1.3 μ (Fig. 9). The meiotic chromosomes in metaphase II of O. *capensis* (Fig. 4) also approach these lengths and as anticipated the bivalents illustrated for O. *cephalotes* (Fig. 5) and O. *herbacea* var. *goetzii* (Fig. 8) average twice as long. The bivalents of O. *duemmeri* (Fig. 6) suggest chromosomes 1.2-2.3 μ long, or slightly longer than those for the others. However, all chromosomes for the species of *Oldenlandia* examined would be considered ± small and, in this regard, are similar to those for all other genera having a basic complement of $x = 9$.

Among the African species of *Oldenlandia* with more than one chromosomal race, four are isostylous and each exhibits a strong weedy tendency. Another species, O. *monanthos*, is not a marked apocrat but the species is heterostylous, while the widespread O. *herbacea* is known with three diploid isostylous varieties and a tetraploid variety which is heterostylous. These data suggest first, that autopolyploidy might be advantageous to a species adapting to new environmental niches and conditions in the tropics. A study of weeds, taking into account chromosomal differences, might lead to an important conclusion regarding the role of autopolyploidy in the success of many pantropical species. A strong correlation certainly exists in *Oldenlandia* between some of the weediest species such as O. *corymbosa*, O. *herbacea* and O. *capensis*, and the occurrence of infraspecific tetraploidy, and the hexa-

ploidy. A second correlation is suggested by these data between the occurrence of heterostyly and autopolyploidy. In addition to the species cited from Africa, all seven species from North America with more than one euploid race are heterostylous. Why such a correlation should exist is at present unknown.

Pollen grains of *Oldenlandia* are small to medium in size (21.3 μ to 32 μ × 19.3 to 30.5 μ), subspheroidal (2-)3- (4-5-) aperturate with long, narrow colpi and simple type A ora, 2.5-5 μ high. These have definite diamond-shaped horizontal limits; less commonly the ora are laterally indefinite or synclinorate. The sexine is thin (1 μ) and finely reticulated, rarely thicker (2 μ) and coarsely reticulated (in *O. lancifolia*), and the nexine is ½ to ⅔ thickness of sexine.

Even though the sample of *Oldenlandia* includes pollen from a number of species they are much alike. The ora are always of the type A but variable in form (Fig. 16a-c). Usually the nexinous thickenings surrounding the ora are readily apparent. An exception to this is the pollen of *O. lancifolia* which has only weak nexinous developments adjacent to the apertures and resembles the pollen of *Kohautia* subg. *Pachystigma*, but pollen of these taxa is readily separable on the basis of size and aperture number. Pollen of *Oldenlandia* is most similar to that of *Amphiasma, Dibrachionostylus* and *Pentodon* among its African allies.

A distinct difference in pollen size between the short- and long-styled flowers of *O. affinis* was noted by Bremekamp (1952). He found that pollen from short-styled plants measure 29.3 μ × 27-30 μ, whereas that from the long-styled plants was only 26 μ × 24-26 μ. For *O. duemmeri* (short style, 25.3 μ × 21.5 μ; long style, 24.0 μ × 21.2 μ) and *O. scopulorum* (short style, 27.3 μ × 24.0 μ; long style, 26.7 μ × 22.0 μ) similar differences have been found in which the pollen from short-styled plants is slightly larger than pollen from long-styled ones. Pollen from short-styled diploid plants of *O. monanthos* average 26.6 μ × 22.0 μ, while pollen from a short-styled octoploid individual is 32.0 μ × 26.7 μ, giving an anticipated larger size for pollen from a polyploid individual than from diploid plants. Both chromosomal and floral differences are also found in *O. herbacea* and pollen available from these plants has the following characteristics: (1) var. *herbacea*, 2*x*, homostylous—25.1 μ × 24.6 μ, sexine thin (1.7 μ), finely reticulated, apertures 2 (40%) or 3; (2) var. *holstii*, 4*x*, short style—30.6 μ × 30.5 μ, sexine as preceding apertures 3 (85%) or 4; (3) var. *holstii*, 4*x*, long style—29.4 μ × 28.4 μ, sexine and apertures as preceding. These results show that not only is the pollen smaller for the diploid plants than for the tetraploid ones, but that the sexine is thinner, more finely reticulated, and with fewer apertures per grain. Similar differences between the pollen of diploid and tetraploid individuals have also been found for *O. corymbosa* (Lewis, 1964), but for this species both chromosomal races are homostylous. However, in *O. herbacea* the tetraploid variety has both long-styled and short-styled forms. The pollen from 4*x* plants of both floral forms is similar except that the pollen from short-styled plants is slightly larger. Many additional African species not studied from this aspect are heterostylous, but the differences may be similar to those already noted in this study and previously reported by Bremekamp (1963) in the tribe *Psychotrieae*. The results clearly show, however, that a mean-

ingful comparison of pollen size and style type without a prior knowledge of the chromosome number of a taxon is difficult.

Pentodon Hochst.

The most obvious character distinguishing *Pentodon* from *Oldenlandia* is the pentamerous flower of *Pentodon*, while the shape of the placenta, the rather thin and flexible capsule wall, the absence of slime formation when seeds are moistened, and the curious swellings of the testa wall are all very difficult criteria of distinction to use with ease. The genus has two African species with *P. laurentioides* Chiov. rare in Somalia and *P. pentandrus* widespread and considered conspecific by Bremekamp (1952) with the American *P. halei* (T. & G.) Gray.

The common *P. pentandrus* is diploid ($n = 9$) and is similar to *P. halei* (Lewis, 1962b). The bivalents illustrated in Fig. 10 are similar in size and number to those of *Oldenlandia herbacea* (Fig. 8) and to other species of *Oldenlandia* not illustrated. The pollen of *P. pentrandrus* is small (22.8 μ × 20 μ), subspheroidal, and 3-aperturate with long, narrow colpi, and simple type A ora, 3.3 μ high, indefinite horizontally. The sexine is thin (1 μ) and finely reticulated, the nexine thinner (0.5 μ). The pollen approximates that of *P. halei, Amphiasma, Dibrachionostylus* and most species of *Oldenlandia.*

II. BASIC CHROMOSOME NUMBER X = 10.

Otomeria Benth.

Verdcourt (1953a) recognized seven species of *Otomeria* and noted close affinities with *Pentas* and *Tapinopentas* and suggested ". . . that all three genera should be united but the result would be heterogeneous as a whole." More recently Hepper (1960) has reduced *Tapinopentas* to synonymy and distributed its species between *Otomeria* and *Pentas.*

The chromosome complements of *O. elatior* ($n = 10$) and *O. guineensis* ($2n = 20$) are based on $x = 10$. Bivalents illustrated for *O. elatior* (Fig. 11) average *ca.* 6 μ in length and are larger than those for all taxa having $x = 9$. This average chromosome length is similar to that of *Pentas* and *Parapentas* and chromosome morphology thus emphasizes the relationship of these genera. In addition, the morphology of the pollen of *O. elatior* is also similar to that of *Pentas* and *Parapentas.*

Parapentas Bremek.

Bremekamp (1952) based *Parapentas* on *Oldenlandia silvatica* K. Sch., which he felt was more closely allied to *Pentas* than to *Oldenlandia.* He recognized three species, which were subsequently revised and added to by Verdcourt (1953b).

The basic chromosome number for *Parapentas* is $x = 10$ (*P. battiscombei,* $2n = 20$; *P. silvatica,* $n =$ ca. 10). The chromosomes are the same size as those

of *Otomeria* and *Pentas*, but larger than *Oldenlandia*, which supports Bremekamp's earlier conclusions. Palynologically these species are similar to those of *Otomeria* and *Pentas*.

Pentas Benth.

In his revision of *Pentas*, Verdcourt (1953c) recognized 32 species which he divided into six subgenera.

The basic number of $x = 10$ for *Pentas*, established earlier (cf. Fagerlind, 1937), was recently confirmed by Lewis (1962b). All previous counts were based on cultivated material. Recently I collected eight taxa in Africa which have been examined cytologically (Appendix 1). These results are in agreement with the earlier data. All taxa are diploid ($n = 10$) excepting *P. lanceolata* subsp. *quartiniana* var. *nemorosa* which is tetraploid ($n = 20$).

Because of many "intermediates" in the *P. lanceolata* complex, Verdcourt (1953c) merged all under *P. lanceolata* and recognized many at the infraspecific level. He mentioned that the subsp. *quartiniana* var. *nemorosa* and the var. *leucaster* both merge with *P. lanceolata* s. s. to form intermediates at the edge of their range. On the basis of known chromosome numbers, the var. *lanceolata* and the var. *leucaster* are diploids while the var. *nemorosa* is tetraploid. Providing individuals typical of var. *nemorosa* are consistently $4x$, then the "intermediates" found by Verdcourt should be triploids and probably sterile. Under these circumstances it is difficult to suggest why so many successful hybridizations exist between the varieties involved in these $2x \times 4x$ crosses. On the other hand, the "intermediates" may represent natural variations of populations which overlap in morphology. This may not be true for all varieties of *P. lanceolata*, but at least for the var. *nemorosa* the population is reproductively isolated from the others and, except for occasional truly triploid intermediates that may be formed, the variability for this taxon is probably inherent. Very often tetraploids are more variable than their diploid ancestors and the tetraploid nature of the var. *nemorosa* is further suggested by a number of characters, e.g., "the var. *nemorosa* is similar to var. *oncostipula* [$2x$] but distinct in the field by virtue of its larger flowers" (Verdcourt, 1953c). Provided that future studies from more individuals substantiate the tetraploidy of var. *nemorosa*, then I believe that the taxon should be recognized at the specific level.

With lengths of about 6 μ for *P. longiflora* (Fig. 12) and *P. zanzibarica* var. *intermedia* (Fig. 13), the bivalents of *Pentas* resemble those of *Otomeria*. They are consistently larger than are the bivalents of those genera with a basic number of 9. *Pentas* is allied to *Otomeria* and *Parapentas* because of both chromosome size and number, and this confirms the conclusions of Bremekamp (1952) and Verdcourt (1953a, 1953b, 1953c).

The pollen of *Pentas* is small to medium (24 $\mu \times 18.7$ μ to 29 $\mu \times 25.5$ μ), 3- (4-5-) aperturate, with long, narrow colpi and type A ora, about 4 μ high, synclinorate or occasionally with the oral belt fading mid-way between the colpi, infrequently with short, horizontal ora. The sexine is 1-1.5 μ thick and reticulations are fine or medium. The nexine is ½ to ⅔ the thickness of the sexine. This

morphology is similar to *Otomeria* and *Parapentas,* particularly in the striking increase in nexine adjacent to the ora.

As already noted for *Agathisanthemum* and *Oldenlandia,* pollen size for short-styled plants may be slightly larger than pollen for long-styled plants. For *P. lanceolata* var. *leucaster* (long style, 22.8 μ × 18.7 μ; short style, 24.0 μ × 20.9 μ), *P. lanceolata* var. *oncostipula* (long style, 22.2 μ × 20.5 μ; short style, 24.8 μ × 21.3 μ) and *P. pubiflora* (long style, 23.0 μ × 20.7 μ; short style, 25.3 μ × 22.6 μ) there are slight increases in pollen size of short-styled flowers over long-styled flowers without other observable differences.

III. BASIC CHROMOSOME NUMBER X = 11.

MANOSTACHYA Bremek.

Two species originally described under *Oldenlandia* form the basis of the genus *Manostachya* (Bremekamp, 1952). According to Bremekamp, the genus is isolated by having reduced axillary inflorescences, short stipular sheaths, subglobose capsules with the upper half superior, testa with thick outer walls forming a network of ridges and rather large pollen. He suggested that *Stephanococcus* (based on *Oldenlandia crepinianus* K. Sch.) is its closest ally. Verdcourt (1958) noted that the seed testa with its network of ridges is quite similar to the pitted testa of members of the tribe *Mussaendeae* grouped in a different subfamily.

The chromosome number of *M. staelioides* is $2n = 44$ which is the only African member of the *Hedyotideae* known with a basic complement of $x = 11$. Mitotic chromosomes from untreated cells measure only 1 μ or less in length (Fig. 14) and are somewhat smaller than those of *Oldenlandia* and other genera based on $x = 9$, and much smaller than those of *Pentas, Parapentas* and *Otomeria.* In size as well as in number the chromosomes of *Manostachya* more closely approximate those of the woody members of the family such as the *Psychotrieae* or even the more distantly related *Mussaendeae. Manostachya* does, however, share the chromosomal number but not the size with the North American species of *Hedyotis* subg. *Edrisia* (Lewis, 1962a). This evidence suggests that this group in North America is the end of an ancient phylad based on $x = 11$. Provided this hypothesis is correct, then *Manostachya* may also represent a second taxon in the *Hedyotideae* having the common rubiaceous set of chromosomes which now exists as a relic complement in the tribe. An additional relic in *Manostachya* may be the ridges or pits found on the outer seed wall, a character unique in the *Hedyotideae* but common to a number of woody (and more primitive ?) tribes in the subf. *Cinchonoideae.*

The pollen of *M. staelioides* is medium (33.3 μ × 28 μ), and 3-(4-) aperturate, with long, narrow colpi and simple type A ora. The sexine is 1.7 μ thick with medium reticulations and the nexine is 1 μ thick, but much thicker adjacent to the ora. This morphology resembles that of most members of the *Hedyotideae.* However, the pollen differs in both size and wall structure from *Stephanococcus,* a genus thought to be allied to *Manostachya,* which has small grains and thin, finely reticulated sexines.

IV. BASIC CHROMOSOME NUMBER UNKNOWN.

It has been impossible to obtain countable cytological material for many known genera of African *Hedyotideae* although pollen from all but two of these has been examined. Most genera not examined cytologically are monotypic with limited distributions and even herbarium material for use in pollen studies is very scarce.

The most important diagnostic features of the pollen for 16 genera are listed in Table 2. Pollen of *Batopedina, Carphalea, Dirichletia, Dolichometra, Diotocranus, Hedythyrsus, Pseudonesohedyotis, Placopoda, Sacosperma, Schismatoclada, Stephanococcus* and *Thecorchus* is essentially similar in aperture morphology: all are 3- or infrequently 4-colporate with long, narrow colpi and simple, type A ora, as already outlined for the majority of members of the tribe. Ora may be synclinorate (A_1) as for *Hedythyrsus, Pseudonesohedyotis* and *Sacosperma,* horizontally indefinite (A_2) as for *Dolichometra,* and *Placopoda,* or horizontally distinct (A_3) as for *Batopedina, Diotocranus, Dirichletia, Schismatoclada,* and *Thecorchus.* The ora of *Carphalea* are typically of type A_2 and those of *Stephanococcus* of type A_3, but for both, synclinorate ora are also found. The sexine is thin (to 1.5 μ) and reticulated, and the grains are small.

Pollen of four genera differ from these. The least different is the very finely reticulated pollen of *Pentanopsis fragrans,* having only slight nexinous thinnings surrounding a type A os. This apparently reduced character is also shared by *Danais* but additionally the os is very narrow and the grains are very small (16 μ × 14 μ), even though the sexine is coarsely reticulated. Somewhat more isolated are the grains of *Nesohedyotis,* which are quite unlike those of supposedly related species of *Hedyotis* from Asia. They are very small (11 μ × 14.6 μ), prolate, with a nexine equal in thickness to the sexine and with apertures having long, broad colpi, and compound ora which possess a faint type A os and a large type B os (3 μ) surrounded by a fine margin. Palynological characters clearly support the elevation of *Hedyotis arborea* to generic rank as *Nesohedyotis arborea* (Bremekamp, 1952). Likewise the pollen of *Hekistocarpa* is prolate in shape, small in size with long, broad colpi. The apertures differ from those of *Nesohedyotis* by the presence of very large (to 8 μ), emarginate ora of type B with no type A os. This aperture type is unique in the *Hedyotideae.*

DISCUSSION

Based on known chromosome complements, the African members of the tribe *Hedyotideae* are separable by number and size into three groups. The largest group of genera is based on $x = 9$ and has small chromosomes (1.1-2.5 μ), another group is based on $x = 10$ and has medium chromosomes (3 μ >) and the third group is based on $x = 11$) and has very small chromosomes (1 μ <). The last is represented in Africa solely by *Manostachya,* even though the complement of $x = 11$ is by far the most common one in this predominantly woody family. However, it is infrequent in the tribe *Hedyotideae* and I suggest that this complement is a relic. The basic complement of $x = 10$ is known for three closely allied genera, *Otomeria, Parapentas* and *Pentas.* They are extant genera of probably an old phylad which

Table 2. Summary of the pollen morphology for 16 African genera of *Hedyotideae* lacking known chromosome numbers.

Genus[a]	Pollen size[b]	Aperture number	Os type[c]	Colpus width[d, e]	Sexine[f]	Reticulation[g]	Shape
Batopedina	small-med.	3	A_3	narrow	thin	medium	subspheroidal
Carphalea	medium	3	$A_2(A_1)$	narrow	medium	medium-coarse	subspheroidal
Danais	small	3	A_2	narrow	thin	coarse	subspheroidal
Diotocranus	medium	3	A_3	narrow	thin	fine	subspheroidal
Dirichletia	medium	4	A_3	narrow	thin	fine	subspheroidal
Dolichometra	medium	3	A_2	narrow-medium	thin	medium	subspheroidal
Hedythyrsus	small	3	A_1	narrow	thin	medium-fine	subspheroidal
Hekistocarpa	small	3	B	broad	thin	fine	prolate
Nesohedyotis	small	3	$(A_2)+B$	broad	thin-medium	medium	prolate
Pentanopsis	medium	4	A_2	narrow	thin	very fine	subspheroidal
Placopoda	small	3	A_2	narrow	thin	medium	subspheroidal
Pseudonesohedyotis	small-med.	3	A_1	narrow	thin	fine	subspheroidal
Sacosperma	small	3	A_1	narrow	thin	medium	subspheroidal
Schismatoclada[h]	small	3-4	A_3	narrow	thin-medium	fine-coarse	subspheroidal
Stephanococcus	small	3	$A_3(A_1)$	narrow	thin	fine	subspheroidal
Theocorchus	small-med.	3	A_3	narrow	thin	fine	subspheroidal

[a] See Appendix 2 for species studied.
[b] Small 10-25 μ, medium 25-50 μ (Erdtman, 1952).
[c] See text for explanation of oral types.
[d] Narrow to 4 μ, broad > 4 μ.
[e] All colpi are long excepting medium in length for *Dolichometra*.
[f] Thin to 1.5 μ, medium 1.6-2.9 μ, course 3.0 μ >.
[g] Very fine or almost smooth, fine with delicate lumina and muri, medium with lumina ca. 2 μ, coarse with lumina ca. 3 μ.
[h] Pollen from short-styled flowers of *S. psychotriodes* mostly 4-aperturate with sexine medium in thickness and coarsely reticulated; from long-styled flowers mostly 3-aperturate with thin sexine finely reticulated.

originated by chromosomal loss from a prototype having $x = 11$. The most common basic number of $x = 9$ is shared by *Agathisanthemum, Amphiasma, Conostomium, Dibrachionostylus, Kohautia, Oldenlandia, Lelya* and *Pentodon,* and the complement probably arose by further reduction in chromosome number from $x = 10$ to $x = 9$. Based on diversity, frequency and geographical distribution of genera, this is the most successful phylad in the *Hedyotideae.*

It is quite possible that the mutations necessary to form each of these hypoaneuploid lines occurred more than once, perhaps in Africa, but certainly elsewhere. In North America, *Hedyotis* subg. *Edrisia* is even more marked by chromosomal reduction than its African allies, i.e., $x = 11, 10, 9, 8, 7, 6$ (Lewis, 1962a), yet there is no evidence to suggest other than in situ chromosomal evolution in the subgenus. This would stress a parallel reduction in chromosome number between members of the tribe in these continents, probably at different times and at different rates, which further suggests an inherent mutable tendency for chromosomal reduction. For other areas and for these and other genera, the information is fragmentary, but the basic complement of nine chromosomes is almost universal, *viz., Arcytophyllum* (South America), *Dentella* (Asia), *Bouvardia* (Central and North America), *Hedyotis* and/or *Oldenlandia* (Asia and Australia), and *Manettia* (Central America). The overall propensity in the *Hedyotideae,* therefore, has been one of stabilization of the basic chromosome number of nine, most likely one of reduction from $x = 11$. By having characteristically two pairs of chromosomes less than the chromosomal "epicenter" of the family at $x = 11$, this largely herbaceous tribe is regarded as chromosomally advanced.

The generalized morphology of the pollen for 28 African genera in the *Hedyotideae* is small- to medium-sized, subspheroidal, infrequently prolate; 3-aperturate, with long and narrow colpi having smooth membranes, and with simple type A ora which may be synclinorate, horizontally indefinite, or distinct in outline; sexine 1-2 μ in thickness, simplibaculate, O-L pattern, with fine to coarse lumina and muri giving variously textured reticulations; nexine $\frac{1}{2}$ to $\frac{2}{3}$ thickness of sexine, rarely equal in thickness, but equatorially much thickened adjacent to the colpi and ora.

This pollen description is characteristic of the taxa examined from the two chromosomally-older groups ($x = 11$ and 10), and widespread among taxa of the $x = 9$ phylad. More complex pollen forms are found only among species of the last group. The typical morphology is probably a basic, primitive condition in the tribe, a conclusion supported by the results of the American species of *Hedyotis* (Lewis, 1965). The larger question of how this pollen morphology relates to the general condition for other tribes in the *Rubiaceae* remains unknown. Is it, for instance, indicative of a specialized and "advanced" level already suggested by the chromosome complement? Will a less specialized morphology be found among members of those tribes known to have the basic chromosome number of $x = 11$? Until a palynological survey is undertaken for the *Rubiaceae* such questions must remain unanswered.

Pollen of some species in the tribe differs strikingly from that of the typical, however, and although such pollen has been described for comparatively fewer

genera, the morphology can be of value in problems relating to intergeneric limits and to phylogenetic studies as a whole. The major variations are summarized under eight criteria: the general pollen form is given first and this is followed (after a dash) by the specialized and/or reduced expression, together with representative taxa.

(1) APERTURE NUMBER: 3-aperturate—4-aperturate in some species of all large genera, in *Dirichletia* and *Pentanopsis;* 5- and infrequently 6- to 8-aperturate in *Kohautia* subg. *Pachystigma;* 2-aperturate is very rare and only known for some pollen of *Oldenlandia herbacea.* A trend to greater frequency of apertures was reported for the pollen of the "advanced" species *Hedyotis rosea* Raf. (Lewis, 1965) and also as an advanced trend for some species of *Dicentra* (Stern, 1962).

(2) APERTURE STRUCTURE, THE COLPUS: long colpus—medium lengths in *Conostomium* subg. *Beckia;* short lengths in *C.* subg. *Conostomium* and subg. *Hockstetteria.*

(3a) APERTURE STRUCTURE, THE OS: simple os, type A, followed by complexity and subsequent reduction—addition of crassimarginate os, type B, in *Agathisanthemum, Lelya* and as reported for *Hedyotis* subg. *Edrisia* (Lewis, 1965); compound os (types A and B) in which the type A os is barely discernible, in *Nesohedyotis* and some species of *Kohautia* subg. *Kohautia;* disappearance of the type A os, leaving only the type B os in other species of *Kohautia* subg. *Kohautia.* This last kind of os was reported for some species of *Hedyotis* subg. *Edrisia* which are thought to represent the most advanced, but highly reduced, elements of that subgenus (Lewis, 1965).

(3b) APERTURE STRUCTURE, THE OS: simple os, type A, followed by reduction—equatorial extensions of the os reduced and barely discernible in *Danais, Kohautia* subg. *Pachystigma, Oldenlandia herbacea* and *Pentanopsis.*

(4) POLLEN SIZE: medium-small (ca. 20-30 μ—very small grains in *Danais, Kohautia* subg. *Kohautia* and *Nesohedyotis,* a trend already noted for the pollen of *Hedyotis rosea* (Lewis, 1965).

(5) POLLEN SHAPE: subspheroidal—oblate in *Hekistocarpa* and *Nesohedyotis.*

(6) SUPRATEGILLAR ELEMENTS: none—with verrucae in *Conostomium* subg. *Conostomium.* Stern (1962) noted that the advanced *Dicentra* subg. *Dactylicapnos* has pollen with verrucate sexines, while the more primitive subgenera have reticulate, foveolate or rugulate sexines.

(7) SEXINE RETICULATION: medium or fine—very fine reticulation (appearing ± smooth) in *Pentanopsis;* coarse reticulation in *Danais, Kohautia* subg. *Pachystigma,* and *Oldenlandia herbacea.* Pollen having coarse reticulations also typifies the most advanced species of *Hedyotis* subg. *Edrisia* (Lewis, 1965).

(8) SEXINE THICKNESS: medium-fine in thickness (1-2 μ)—thick sexine with associated coarse baculae in *Conostomium* subg. *Conostomium, C.* subg. *Hochstetteria, Kohautia* subg. *Kohautia* and *Lelya.* Thicker sexines were also reported among the most advanced species in *Hedyotia* subg. *Edrisia* (Lewis, 1965).

Other modifications in pollen which might be added include the extremely large os (type B) with a reduced margin in *Hekistocarpa.* Pollen of this genus also

has very broad colpi as does pollen from *Nesohedyotis*. These expressions are most exceptional among members of the *Hedyotideae* and require additional study and confirmation.

It is obvious that the majority of these modifications characterize only a few taxa. If a value of "0" represents the typical expression for each of the pollen characters noted above, "1" represents the atypical expression for each, and values of "2" and "3" for additional alternatives of aperture number and oral structure, then the taxa can be ranked according to their divergence from the typical pollen form. Summarizing for the *Hedyotideae* of Africa, where "0" represents the typical pollen morphology, 28 genera with the number of species examined given in parenthesis rank as follows:

"0-0.6"—*Amphiasma* (2), *Batopedina* (1), *Carphalea* (2), *Dibrachionostylus* (1), *Diotocranus* (1), *Dirichletia* (1), *Dolichometra* (1), *Hedythyrsus* (1), *Manostachya* (1), *Oldenlandia* (13), *Otomeria* (1), *Parapentas* (2), *Pentas* (3), *Pentodon* (1), *Placopoda* (1), *Pseudonesohedyotis* (1), *Sacosperma* (1), *Schismatoclada* (2), *Stephanococcus* (1), *Theocorchus* (1).

"1.3-1.5"—*Agathisanthemum* (3), *Lelya* (1).

"2.7-3.0"—*Conostomium* (4), *Danais* (2), *Pentanopsis* (1).

"4.0" —*Hekistocarpa* (1), *Kohautia* (20), *Nesohedyotis* (1).

The genera most removed palynologically from the generalized morphology are, therefore, *Conostomium, Danais, Hekistocarpa, Kohautia, Nesohedyotis* and *Pentanopsis*, with *Agathisanthemum* and *Lelya* less strikingly so.

It is also relevant to know whether or not these genera exhibiting specialized and/or reduced expressions for pollen are characterized by unique sporophytic expressions. By and large the African representatives of the tribe are herbs with bisexual, homostylous or heterostylous flowers having small or medium corollas and with many, wingless seeds in readily dehiscent capsules. Departures from this morphology are found for *Kohautia* (short-styled flowers only), *Conostomium* (typically long-styled flowers only and greatly enlarged corollas), *Lelya* (tardily dehiscent, nut-like capsules with few seeds), *Nesohedyotis* (small trees with unisexual flowers), *Pentanopsis* (shrubs with large corollas), *Danais* (winged seeds [transferred from the tribe *Cinchoneae* and considered rather isolated by Bremekamp, 1952]) and *Hekistocarpa* (shrub).

Hence there is a marked correlation between genera illustrating atypical male gametophytic characters on the one hand with those having atypical sporophytic characters on the other. A similar correlation, often involving the same features for plants of both generations, was also observed for the North American members of the tribe (Lewis, 1965).

The value of palynological and chromosomal data as an aid to classification has been demonstrated for the North American members of the *Hedyotideae* (Lewis, 1962a, 1965). In Africa the unique chromosome complement of $x = 11$ for *Manostachya* supports the isolated position of this genus in relation to *Oldenlandia*

(Bremekamp, 1952). The chromosome complement of $x = 10$ also supports a position for *Parapentas* in the immediate vicinity of *Otomeria* and *Pentas* rather than with *Oldenlandia* as concluded by Bremekamp (1952).

Agathisanthemum, Conostomium, Kohautia, Lelya and *Nesohedyotis* each possesses a pollen morphology different from all known species of *Oldenlandia* and *Hedyotis* in Afro-Asia. These palynologically distinct genera should not be included in *Oldenlandia* or *Hedyotis,* as they have been until Bremekamp's (1952) recent revision. Palynological data also support the generic rank for *Pentanopsis,* a genus which should be considered part of the oldenlandiaceous group allied to *Kohautia.* Two genera, *Danais* and *Hekistocarpa,* never closely associated with *Oldenlandia,* possess a number of pollen characteristics unknown to *Oldenlandia* and its immediate allies, and palynologically these genera are not closely associated with the epicenter of the tribe. Finally, the pollen morphology of *Schismatoclada* supports its transfer from the *Cinchoneae* to the *Hedyotideae* (Verdcourt, 1958).

No variation in pollen and chromosomal morphology parallels the gross morphology characteristics used in separating *Amphiasma, Dibrachionostylus* and *Pentodon* from *Oldenlandia.* Obviously the absence of cytopalynological characteristics does not automatically relegate these genera to subdivisions of *Oldenlandia.* The similarity does indeed suggest that too much emphasis might have been placed on certain exo- and endomorphic criteria of only secondary value in delimiting genera. A re-evaluation in these instances is required. The genus *Amphiasma* is distinguished from *Oldenlandia* only by its dorsiventrally flattened seeds and tubular stipules, yet the latter character is weakened by the reduced stipular sheath known for *A. divaricantum* (Engl.) Bremek. The shape of the seed is in itself a minor difference on which to base genera, particularly when this is not accompanied by alterations in the testal cells or by craters, hilar ridges or others. In my opinion *Amphiasma* would be better accommodated as a subgroup of *Oldenlandia.* The same judgment applies to *Dibrachionostylus:* loculicidally and septicidally dehiscent capsules of *Oldenlandia* are insufficient evidence for generic separation. This monotypic genus should be replaced in *Oldenlandia.*

Apart from having pentamerous flowers and swellings on the lateral testal walls, the remaining criteria (p. 194) separating *Pentodon* from *Oldenlandia* are of secondary value. Moreover the unusual testal swellings known for *P. pentandrus* and *P. halei* are not found to the same extent for *P. laurentioides* Chiov. and their near absence in this species clearly decreases the generic importance of this specialization. Perhaps the closest allies of *Pentodon,* however, are Asian and Oceanic in origin, and until these can be studied in detail, the genus should be retained.

The differences in pollen and/or sporophytic morphology of some additional genera (e.g., *Eionitis*) are not significant enough to separate them from *Oldenlandia* and this suggests that an even more conservative treatment for members of the tribe *Hedyotideae* in Africa is in order when more material is available for cytological and comparative morphological studies. Additional research, particularly of Asian taxa, is necessary before far-reaching changes in classification can be made.

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Appendix 1

Procedures, Materials and Results of Chromosomal Study

Immature flower buds were fixed in 4 parts chloroform, 3 parts absolute ethanol and 1 part glacial acetic acid, and airmailed from Africa to England for storage at -40°C. From one to seven months following fixation, whole buds were squashed in 2% acetic-orcein and those preparations showing pollen mother cell meiosis were mounted in euparal for permanent reference.

To supplement the chromosome counts obtained from field collections, seeds obtained directly from Africa or from herbarium specimens were sown at the Royal Botanic Gardens, Kew. At maturity the apical meristems or whole buds from these plants were treated as above for both mitotic and meiotic counts. Seeds from some species remained viable on herbarium sheets for periods up to five years.

Voucher specimens for my collections, including those from natural and greenhouse conditions, are deposited at the Missouri Botanical Garden (MO) and, with

a few exceptions, at the Royal Botanic Gardens (K) and the U. S. National Museum (US). For each successful count, the original locality of the collection, the collector and number and the locality of the herbarium voucher, if other than the author's, are given below under the appropriate taxa. Following these data the number of plants examined for each count is given in parentheses together with a notation of the seed source when applicable. The genera and subgenera are arranged alphabetically.

Taxon	*n*	2*n*	Locality and voucher
AGATHISANTHEMUM			
A. bojeri Klotzsch subsp. *bojeri*	9	18	TANGANYIKA: Tanga Region, Tanga Area, 5.2 miles N. of Tanga, *Lewis 6056* (1); 16 miles W. of Tanga, *Lewis 6063* (1).
A. bojeri subsp. *australe* Bremek.	—	18	S. AFRICA: Natal, Hlabisa Dist., Charters Creek, *Lewis 6299* (2).
A. globosum (Hochst. ex A. Rich.) Klotzsch ex Bremek.	—	36	KENYA: Rift Valley Prov., West Suk Dist., 0.3 miles N. of Keringet, *Lewis 5987* (1). N. RHODESIA: N. W. Prov., Mwinilunga Dist., Zambesi River rapids, 4 miles N. of Kalene mission, *Lewis 6209* (1).
AMPHIASMA			
A. merenskyanum Bremek.	—	18	S. W. AFRICA: Kaokoveld Dist., 6 miles N. of Kamanjob, *De Winter & Leistner 5103* (K) (1[1]).
A. sp.	—	ca.36	S. W. AFRICA: Walvis Bay Dist. E. edge of Namid Desert, *Lewis 6396* (1[2]).
CONOSTOMIUM subg. BECKIA			
C. kenyense Bremek.	—	ca.36	KENYA: S. Prov., Machakos Dist., 44 miles from Thika, Yatta, *Archer 88* (K) (1[1]).
CONOSTOMIUM subg. HOCHSTETTERIA			
C. natalense (Hochst.) Bremek.	9	18	S. AFRICA: Cape, Bizana Dist., 16 miles W. of Bizana, *Lewis 6370* (2[2]); Transvaal, Barberton Dist., 25.8 miles S. E. of Barberton, *Lewis 6332* (1). SWAZILAND: Mbabane, Ukutula, *Lewis 6321* (3).
DIBRACHIONOSTYLUS			
D. kaessneri (S. Moore) Bremek.	9	—	KENYA: Central Prov., Nairobi National Park, *Lewis 5904* (2).
KOHAUTIA subg. KOHAUTIA			
K. aspera (Heyne ex Roth) Bremek.	18	36	ETHIOPIA: Harar Prov., N. E. edge of Lake Alemaya, *Lewis 5874* (4).
K. caespitosa Schnizl. var. *caespitosa*	—	36	S. AFRICA: Natal, Hlabisa Dist., 14 miles N. W. of Hluhluwe, *Lewis 6311* (1).
K. caespitosa var. *ameniensis* (K. Krause) Bremek.	—	36	TANGANYIKA: Tanga Region, Lushoto Area, Mombo-Lushoto Rd., *Samsei 3070* (K) (1[1]).
K. coccinea Royle var. *coccinea*	9	18	ETHIOPIA: Harar Prov., Collubi, *Lewis 5900* (2).
K. coccinea var. *macrodonta* (Bak.) Bremek.	—	18	KENYA: Rift Valley Prov., Trans Nzoia Dist., E. N. E. slope of Mt. Elgon, *Lewis 5952* (2).

Taxon	n	2n	Locality and voucher
K. cynanchica DC.	9	18	SWAZILAND: 2.5 miles N. of Golela, *Lewis 6313* (3).
K. grandiflora DC.	9	—	UGANDA: N. Prov., Karamoja Dist., 4 miles N. E. of Irire, *Lewis 5997* (3); 7 miles W. of Namalu prison, base of Mt. Oboa, *Lewis* 5990 (1).
KOHAUTIA subg. PACHYSTIGMA			
K. longifolia Klotzsch var. *longifolia*	—	36	N. RHODESIA: N. Prov., Abercorn Dist., Sunzu Gorge, *Lewis 6094* (3[1]).
K. virgata (Willd.) Bremek.	27	54	S. AFRICA: Natal, Hlabisa Dist., Charters Creek, *Lewis 6294* (2); Transvaal, Pretoria Dist., Pretoria, Wonderboom, *Lewis 6348* (1); Transvaal, W. of Pretoria, *Lewis 6356* (1[2]). S. RHODESIA: Nuanetsi Dist., Nuanetsi River, *Drummond & Rutherford-Smith 7554* (SRGH) (2[1]).
LELYA			
I. prostrata (R. Good) W. H. Lewis var. *prostrata*	18	—	TANGANYIKA: S. Highlands Region, Iringa Area, 4.5 miles N. E. of John's Corner, *Lewis 6067* (2).
MANOSTACHYA			
M. staelioides (K. Sch.) Bremek.	—	44	N. RHODESIA: N. W. Prov., Solwezi Dist., 1 mile S. E. of Solwezi, *Lewis 6128* (2).
OLDENLANDIA subg. ANEURUM			
O. lancifolia (Schumach.) DC. var. *lancifolia*	18	—	CAMEROUN: 36 km. N. E. of Douala, *Lewis 6407* (1[2]). KENYA: Central Prov., Embu Dist., Embu, *Lewis 5905* (1).
O. lancifolia var. *scabridula* Bremek.	18	—	N. RHODESIA: N. W. Prov., Mwinilunga Dist., Mujileshi River, 5-6 miles S. E. of Angola—N. R. border, *Lewis 6167* (1).
OLDENLANDIA subg. ANOTIDOPSIS			
O. angolensis K. Sch.	9	—	N. RHODESIA: N. Prov., Abercorn Dist., Chila Lake, Abercorn, *Lewis 6123* (1).
	18	—	N. RHODESIA: N. W. Prov., Mwinilunga Dist., Zambesi River, 4 miles N. of Kalene mission, *Lewis 6201* (2).
O. cephalotes (Hochst.) O. Ktze.	9	—	SWAZILAND: Mbabane, Mbabane River, *Lewis 6314* (1).
	—	36	SWAZILAND: Komati River by Forbes Reef-Piggs Peak Rd., *Lewis 6331* (1).
O. goreensis (DC.) Summerhayes	18	36	ANGOLA: Moxico Dist., 2 miles W. of Jimbe River by Caianda-Mwinilunga Rd., *Lewis 6213* (1). KENYA: Rift Valley Prov., Trans Nzoia Dist., Kitale, *Lewis 5980* (2). N. RHODESIA: N. Prov., Abercorn Dist., 5.5 miles S. W. of Abercorn, *Lewis 6120* (1); N. W. Prov., Mwinilunga Dist., 1-4 miles E. of Angola-N. R. border, *Lewis 6132* (1). TANGANGYIKA: W. Region, Kigoma Area, Kasoji, *Newbould & Harley 4419* (1[1]). UGANDA: Buganda Prov., Mengo Dist., 3.5 miles N. E. of Kampala, *Lewis 6022* (1).

Taxon	n	$2n$	Locality and voucher
Oldenlandia subg. Cephalanthium			
O. scopulorum Bullock var. *scopulorum*	9	—	KENYA: Rift Valley Prov., Laikipia Dist., 3 miles W. of Thomson's Falls, *Lewis 6950* (1).
O. scopulorum var. *lanceolata* Bremek.	9	—	KENYA: Rift Valley Prov., Naivasha Dist., Lake Naivasha, *Lewis 5949* (2).
Oldenlandia subg. Hemicephalum			
O. saxifragoides Chiov.	—	18	SOMALIA: Eil, *Hemming 1673* (K) (2^1).
Oldenlandia subg. Hymenophyllum			
O. echinulosa K. Sch.	9	18	TANGANYIKA: S. Highlands Region, Rungwe Area, S. slopes of Poroto Mts., *Lewis 6091* (2).
O. pellucida Hiern	—	18	TANGANYIKA: W. Region, Mpanda Area, Belengi, 12 miles N. of Kasogi, *Harley 9137* (K) (2^1).
Oldenlandia subg. Octoneurum			
O. affinis (Roem. & Schult.) DC.	—	18	CONGO (BRAZZA.): Diosso, *Lewis 6402* (2^2). GHANA: E. Region, Accra Dist., Legon, *Lewis 6419* (1^2). NIGERIA: W. Region, Benin Prov., Iyekuselu Dist., W.A.I.F.O.R., *Daramola s. n.* (FHI) (2^1). S. AFRICA: Natal, Port Shepstone Dist., nr. Port Edward, *Lewis 6366* (2^2); Natal, Hlabisa Dist., Charters Creek, *Lewis 6298* (2). INDIA: Hyderabad, Warangal, *Lewis 6375* (1^2).
Oldenlandia subg. Oldenlandia			
O. capensis L. f. var. *capensis*	9	18	ANGOLA: Moxico Dist., 2 miles W. of Jimbe River by Caianda-Mwinilunga Rd., *Lewis 6214* (2). N. RHODESIA: N. W. Prov., Mwinilunga Dist., Mujileshi River, 5-6 miles S. E. of Angola-N. R. border, *Lewis 6173* (1). TANGANYIKA: Tanga Region, Tanga Area, 4 miles N. of Tanga, *Lewis 6059* (1).
	—	36	N. RHODESIA: S. Prov., Livingstone Dist., Livingstone I., Victoria Falls, *Lewis 6249* (2).
O. capensis var. *pleiosepala* Bremek.	9	18	N. RHODESIA: N. W. Prov., Mwinilunga Dist., 4 miles N. of Kalene mission, *Lewis 6210* (2).
	9, 18	—	N. RHODESIA: N. W. Prov., Mwinilunga Dist., West Lunga River nr. Mwinilunga, *Lewis 6131* (2, 2*x*; 1, 4*x*).
O. corymbosa L. var. *corymbosa*	9	18	Based on 7 collections from CAMEROUN, DAHOMEY, GABON, NIGERIA, TOGO, BRAZIL (cf. Lewis, 1964).
	18	36	Based on 13 collections from ETHIOPIA, KENYA, NIGERIA, INDIA (cf. Lewis, 1964).
	27	54	Based on 1 collection from TOGO (cf. Lewis, 1964).

Taxon	n	2n	Locality and voucher
O. *corymbosa* var. *subpedunculata* O. Ktze.	18	35	Based on 6 collections from KENYA, S. RHODESIA, TANGANYIKA (cf. Lewis, 1964).
O. *fastigiata* Bremek.	—	18	TANGANYIKA: Tanga Region, Handeni Area, 9 miles S. W. of Handeni, *Lewis 6064* (2[1]).
O. *herbacea* (L.) Roxb. var. *herbacea*	9	18	KENYA: Central Prov., Nairobi National Park, *Lewis 5905* (1). N. RHODESIA: N. Prov., Abercorn Dist., 2 miles S. W. of Abercorn, *Lewis 6122* (1); N. W. Prov., Mwinilunga Dist., 1 mile E. of Ikelengi, *Lewis 6190* (1); Zambesi River, 4 miles N. of Kalene mission, *Lewis 6202* (1). S. RHODESIA: Salisbury Dist., Salisbury, Cranborne, *Lewis 6251* (2). UGANDA: Buganda Prov., Entebbe Dist., 4 miles N. E. of Entebbe, *Lewis 6017* (2). SWAZILAND: Komati River by Forbes Reef-Piggs Peak Rd., *Lewis 6328* (1); Mbabane, Mbabane River, *Lewis 6315* (1).
O. *herbacea* var. *flaccida* Bremek.	9	—	ETHIOPIA: Harar Prov., 1.8 km. W. of Errer River by Harar-Giggiga Rd., *Lewis 5861* (2). CONGO(LÉOP.): Katanga Prov., Lualaba Dist., 13 miles S. S. W. of Mutschatsha, *Lewis 6237* (2).
O. *herbacea* var. *goetzei* Bremek.	9	18	CONGO(LÉOP.): Katanga Prov., Lualaba Dist., 15 miles N. N. W. of Kalene mission, *Lewis 6228* (2); 13 miles S. S. W. of Mutschatsha, *Lewis 6238* (2).
O. *herbacea* var. *holstii* (K. Sch.) Bremek.	—	36	KENYA: Coast Prov., Taita Dist., S. E. slope of Mt. Vuria, *Lewis 5931* (3).
O. *linearis* DC.	9	18	KENYA: Rift Valley Prov., Trans Nzoia Dist., Kitale, *Lewis 5979* (2); E. N. E. slope of Mt. Elgon, *Lewis 5953* (2), *5977* (1). TANGANYIKA: W. Region, Kigoma Area, Kasoje, *Newbould & Harley 4415* (K) (1[1]). UGANDA: N. Prov., Karamoja Dist., 7 miles W. of Namalu, *Lewis 5991* (1).
O. *marginata* Bremek.	—	36	KENYA: Coast Prov., Lamu Dist., Osina, *Greenway & Rawlings 9289* (K) (2[1]).
O. *praetermissa* Bremek.	18	36	GHANA: E. Region, Accra, *Lewis 6416* (2[2]).
O. cf. *pumila* (L. f.) DC.	9	18	UGANDA: W. Prov., Toro Dist., Queen Elizabeth National Park, N. W. shore of Lake Edward, *Lewis 6009* (3).
O. *pumila* (L. f.) DC.	—	18	INDIA: Hyderabad, Osmania University campus, *Lewis 6376* (2[2]).
O. *somala* Chiov. ex Bremek.	—	36	TANGANYIKA: Lake Region, Musoma Area, Nata Rest House, *Tanner 4121* (K) (3[1]).
OLDENLANDIA subg. OROPHILUM			
O. *johnstonii* (Oliv.) K. Sch.	—	18	KENYA: Central Prov., Nairobi National Park, *Lewis 5906* (1).

Taxon	n	2n	Locality and voucher
O. monanthos (Hochst. ex A. Rich.) Hiern	9	18	ETHIOPIA: Harar Prov., Collubi, *Lewis 5899* (2); 3 km. E. of Gara Ades, *Lewis 5880* (1).
	27	—	KENYA: Nyanza Prov., Kericho Dist., S. W. Mau Forest, *Kerfoot 2781* (K) (1[1]).
	36	—	KENYA: Rift Valley Prov., Trans Nzoia Dist., E. N. E. slope of Mt. Elgon, *Lewis 5955* (2).
O. rupicola (Sand.) O. Ktze.	9	18	TANGANYIKA: Tanga Region, Lushoto Area, Herkulu Tea Estate, ca. 7 miles E. of Soni, *Lewis 6051* (3).
OLDENLANDIA subg. POLYCARPUM			
O. duemmeri S. Moore	9	—	UGANDA: Buganda Prov., Entebbe Dist., 4 miles N. E. of Entebbe, *Lewis 6018* (2).
OLDENLANDIA subg. STACHYANTHUS			
O. flosculosa Hiern	—	36	ZANZIBAR: Cheraka, mile 1b, *Faulkner 2536* (K) (2[1]).
OTOMERIA			
O. elatior (A. Rich. ex DC.) Verdc.	10	—	ANGOLA: Moxico Dist., 2 miles W. of Jimbe River on Caianda-Mwinilunga Rd., *Lewis 6215* (3). N. RHODESIA: N. Prov., Abercorn Dist., Sunzu Gorge, *Lewis 6097* (1). UGANDA: Buganda Prov., Mengo Dist., 3.5 miles N. E. of Kampala, *Lewis 6024* (2).
O. guineensis Benth.	—	20	LIBERIA: Monrovia, *Wrigley & Melville 703* (K) (3[1]).
PARAPENTAS			
P. battiscombei Verdc.	—	20	KENYA: Central Prov., Meru Dist., vicin. of Chogoria, *Lewis 5914* (2[1]).
P. silvatica (K. Sch.) Bremek.	ca. 10	—	TANGANYIKA: Tanga Region, Lushoto Area, ca. 7 miles E. of Soni, *Lewis 6049* (1).
PENTAS			
P. lanceolata (Forsk.) Deflers	—	20	S. AFRICA: Natal, Port Shepstone Dist., Mtamvuna River, nr. Port Edward, *Lewis 6367* (1[2]).
P. lanceolata subsp. *lanceolata* var. *lanceolata*	10	—	KENYA: Rift Valley Prov., Naivasha Dist., 10 miles E. of Naivasha, *Lewis 5928* (2).
P. lanceolata subsp. *quartiniana* (A. Rich.) Verdc. var. *leucaster* (Krause) Verdc.	10	—	KENYA: Coast Prov., Taita Dist., S. E. face of Mt. Vuria, *Lewis 5930* (2); Rift Valley Prov., Trans Nzoia Dist., Kitale, *Lewis 5982* (1).
P. lanceolata subsp. *quartiniana* var. *nemorosa* (Chiov.) Verdc.	20	—	KENYA: Central Prov., Embu Dist., 2 miles N. E. of Runyenje's, *Lewis 5910* (2).
P. lanceolata subsp. *quartiniana* var. *oncostipula* (K. Sch.) Verdc.	—	20	TANGANYIKA: Tanga Region, Lushoto Area, ca. 7 miles E. of Soni, *Lewis 6040* (1).

Taxon	*n*	2*n*	Locality and voucher
P. longiflora Oliv.	10	—	KENYA: Central Prov., Meru Dist., 5 miles S. of Kanyekine, *Lewis 5915* (2); Rift Valley Prov., Trans Nzoia Dist., E. N. E. slope of Mt. Elgon, *Lewis 5956* (1).
P. longiflora f. *glabrescens* Verdc.	10	—	KENYA: Rift Valley Prov., Trans Nzoia Dist., E. N. E. slope of Mt. Elgon, *Lewis 5962* (2).
P. pubiflora S. Moore	10	—	KENYA: Rift Valley Prov., Trans Nzoia Dist., E. N. E. slope of Mt. Elgon, *Lewis 5963* (2).
P. zanzibarica (Klotzsch) Vatke var. intermedia Verdc.	10	—	UGANDA: W. Prov., Toro Dist., Bunyangabu Co., nr. Nyakalengija, *Lewis 6005* (2).
PENTODON			
P. pentandrus (Schum. & Thonn.) Vatke var. *pentandrus*	9	—	TANGANYIKA: Tanga Region, Tanga Area, 7 miles N. of Tanga, *Lewis 6055* (1). UGANDA: Buganda Prov., Mengo Dist., Kampala, King's Lake, *Lewis 6027* (1).

[1] Seeds obtained from herbarium specimens; the chromosomal voucher is in most cases the original collection.

[2] Seeds sent by Mr. S. R. J. White from Africa or Mr. B. Bahadur from India; the chromosomal voucher is from greenhouse-matured seedlings.

APPENDIX 2

Palynological Procedures and Materials

Whole flowers, mature buds, or anthers only were removed from herbarium specimens and acetolyzed according to the procedure outlined by Erdtman (1952). Most collections were also chlorinated before being mounted in glycerin jelly and sealed with paraffin. A complete set of slides is maintained at the Missouri Botanical Garden and duplicates of many are filed with either the Palynological Laboratory, Stockholm-Solna, or the Royal Botanic Gardens, Kew.

Palynological terminology follows Erdtman (1952) and Lewis (1965). Measurements for quantitative characters are based on 10 random samples with the average of these given throughout the descriptions.

Herbarium vouchers of my collection are deposited at the Missouri Botanical Garden (MO), the Royal Botanic Gardens (K) and the U. S. National Museum (US). Collections of others are with these institutions or with the Naturhistoriska Riksmuseum, Stockholm (S) as indicated. The genera and species studied are listed alphabetically below together with the collector and number, herbarium where specimen filed (excepting the author's) and the country of collection.

Agathisanthemum bojeri Klotzsch subsp. *bojeri, Lewis 6056* (Tanganyika). *A. globosum* (Hochst. ex A. Rich.) Klotzsch ex Hiern, *Irwin 237* (K) (Kenya). *A quadricostatum* Bremek., *Richards 1369* (K) (N. Rhodesia).

Amphiasma benguellense (Hiern) Bremek., *Grossweiler 9686* (K) (Angola). *A. merenskyanum* Bremek., *Dinter 6836* (S) (S. W. Africa).

Batopedina linearifolia (Bremek.) Verdc., *Fanshawe 4143* (K) (N. Rhodesia).

Carphalea madagascariensis Lam., *Afzelius s. n.* (S) (Madagascar). *C. pervilleana* H. Brown, *Afzelius s. n.* (S) (Madagascar).

Conostomium kenyense Bremek., *Adamson B3564* (K) (Kenya). *C. longitubum* (Beck) Cuf., *White 175* (K) (Somalia). *C. natalense* (Hochst.) Bremek., *Lewis 6321* (Swaziland). *C. quadrangulare* (Rendle) Cuf., *Napier 2067* (K) (Kenya).

Danais fragrans Comm. ex Gaertn., *Anderson 103* (S) (Mauritius).

Dibrachionostylus kaessneri (S. Moore) Bremek., *Lewis 5904* (Kenya).

Diotocranus lebrunii Bremek., *Robinson 4548* (K) (N. Rhodesia).

Dirichletia sp., *Newbould 3509* (S) (Kenya).

Dolichometra leucantha K. Sch., *Drummond & Hemsley 3449* (K) (Tanganyika).

Hedythyrsus thamnoideus (K. Sch.) Bremek., *Dale 667* (K) (Congo, Léop.).

Hekistocarpa minutiflora Hook. f., *Dusén s. n.* (S) (Cameroon), FHI 30613 (K) (Nigeria).

Kohautia amatymbica Eckl. & Zeyh., *Methuen 131* (K) (S. Rhodesia). *K. angolensis* Bremek., *Pearson 2382* (K) (Angola). *K. aspera* (Heyne ex Roth) Bremek., *Lewis 5858* (Ethiopia). *K. caespitosa* Schnizl., *Lewis 6311* (S. Africa). *K. coccinea* Royle, *Lewis 5952* (Kenya). *K. cuspidata* (K. Sch.) Bremek., *Wild 4762* (K) (S. Rhodesia). K. cynanchica DC., *Lewis 6313* (Swaziland). *K. effusa* (Oliv.) Bremek., *Anderson 1046* (K) (Kenya). *K. grandiflora* DC., *Lewis 5990* (Uganda). *K. lasiocarpa* Klotzsch, *Chase 5922* (K) (S. Rhodesia). *K. longifolia* var. *longifolia, Lewis 6094* (N. Rhodesia). *K. obtusiloba* (Hiern) Bremek., *Faulkner 810* (K) (Tanganyika). *K. omahekensis* (K. Krause) Bremek., *Lugard 111* (K) (S. Rhodesia). *K. platyphylla* (K. Sch.) Bremek., *Reynolds B9244* (K) (Ethiopia). *K. prolixipes* (S. Moore) Bremek., *Jex-Blake 16* (K) (Kenya). *K. ramosissima* Bremek., *Leistner 2248* (K) (S. Africa). *K. raphidophylla* Bremek., *Pearson 4682* (K) (S. Africa). *K. senegalensis* C. & S., *Brooks 7* (K) (Gambia). *K. somaliensis* Bremek., *Glover & Gilliland 301* (K) (Somalia). *K. virgata* (Willd.) Bremek., *Lewis 6294* (S. Africa).

Lelya prostrata (R. Good) W. H. Lewis var. *prostrata, Lewis 6067* (Tanganyika).

Manostachya staelioides (K. Sch.) Bremek., *Lewis 6128* (N. Rhodesia).

Nesohedyotis arborea (Roxb.) Bremek., *Kerr 8* (K) (St. Helena).

Oldenlandia capensis L. f., *Lewis 6214* (Angola). *O. cephalotes* (Hochst.) O. Ktze., *Lewis 6314* (Swaziland). *O. corymbosa* L. var. *corymbosa* and var. *subpedunculata* O. Ktze., (cf. Lewis, 1964). *O. duemmeri* S. Moore, *Lewis 6018* (Uganda). *O. echinulosa* K. Sch., *Lewis 6091* (Tanganyika). *O. goreënsis* (DC.) Summerhayes, *Lewis 6120* (N. Rhodesia). *O. herbacea* (L.) Roxb. var. *herbacea, Lewis 6251* (S. Rhodesia); *var. holstii* (K. Sch.) Bremek., *Lewis 5931* (Kenya). *O. johnstonii* (Oliv.) K. Sch., *Lewis 5906* (Kenya). *O. lancifolia* (Schumach.) DC. var. *scabridula* Bremek., *Lewis 6023* (Uganda). *O. linearis* DC., *Lewis 5979* (Kenya). *O. monanthos* (Hochst. ex A. Rich.) Hiern, *Lewis 5899* (Ethiopia), *Lewis 5955* (Kenya). *O. praetermissa* Bremek., *Lewis 6416* (Ghana). *O. rupicola* (Sond.) O. Ktze., *Lewis 6051* (Tanganyika). *O. scopulorum* Bullock, *Lewis 5949* (Kenya).

Otomeria elatior (A. Rich. ex DC.) Verdc., *Lewis 6024* (Uganda).

Parapentas battiscombei Verdc., *Lewis 5914* (Kenya). *P. silvatica* (K. Sch.) Bremek., *Lewis 6049* (Tanganyika).

Pentanopsis fragans Rendle, *Ellis 125* (K) (Ethiopia).

Pentas lanceolata (Forsk.) Deflers subsp. *lanceolata* var. *lanceolata, Lewis 5928* (Kenya); subsp. *quartiniana* (A. Rich.) Verdc. var. *leucaster* (Krause) Verdc., *Lewis 5930* (Kenya); subsp. *quartiniana* var. *oncostipula* (K. Sch.) Verdc., *Lewis 6340* (Tanganyika). *P. pubiflora* S. Moore, *Lewis 5963* (Kenya). *P. zanzibarica* (Klotzsch) Vatke var. *intermedia* Verdc., *Lewis 6005* (Uganda).

Placopoda virgata Balf. f., *Bent s. n.* (K) (Socotra).

Pentodon pentandrus (Schum. & Thonn.) Vatke, *Lewis 6055* (Tanganyika).

Pseudonesohedyotis bremekampii Tennant, *Bruce 700* (K) (Tanganyika).

Sacosperma paniculatum (Benth.) G. Taylor, *Louis 13166* (S) (Congo, Léop.).

Schismatoclada citrifolia (Lam. ex Poir.) Homolle, *Decary 10444* (S) (Madagascar). *S. psychotrioides* Baker, *Baron 189, 1769* (K) (Madagascar).

Stephanococcus crepinianus (K. Sch.) Bremek., *Louis 2037* (K) (Congo, Léop.).

Thecorchus wauensis (Schweinf. ex Hiern) Bremek., *Adams 3918* (K) (Ghana).

TYPE COLLECTIONS OF AFRICAN RUBIACEOUS TAXA AT THE MISSOURI BOTANICAL GARDEN HERBARIUM

By Walter H. Lewis

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Shortly after arriving at the Missouri Botanical Garden I was astounded to find so many type specimens of African species housed in the herbarium. My interests include members of the rubiaceous tribe *Hedyotideae* and more particularly *Oldenlandia* and its immediate allies (cf. this issue p. 182). Provided that the representation for these genera is indicative of others, and there is no reason to assume otherwise, then the type collections are numerous enough to be a major source of reference for all students of African botany. Most type specimens are based upon collections made early in the 19th century, notably by W. Schimper (1835-42) from northeastern Africa and by J. F. Drège (1826-34) and F. Krauss (1838-40) from South Africa.

Below are listed the type collections for 26 taxa in *Oldenlandia* and closely allied genera (base chromosome number $x = 9$). Judging from Bremekamp's monographic treatment of *Oldenlandia* (Verh. K. Nederl. Akad. Wetensch., Afd. Natuurk., sect. 2, **48:** 1-297. 1952) this is probably one of the longest lists which can be assembled for these taxa from any herbarium outside of Europe, and certainly in the New World. Prior to this time, not one of the collections had been marked as type material and fewer than half had been stamped as belonging to MO.

1. *Amphiasma robijnsii* Bremek.: *Robyns 2186*, 29 Apr. 1926, Congo (Léop.), MO 1615052.

2. *Crusea ? acuminata* E. Mey. ex Drège, nomen: *Drège s. n.*, South Africa, Natal, MO 1801948. = *Conostomium natalense* (Hochst.) Bremek. var. *glabrum* Bremek.

3. *Hedyotis abyssinica* Hochst. ex A. Rich.: *Schimper 1902*, 10 Oct. 1842, Ethiopia, MO 1801939. = *Kohautia coccinea* Royle.

4. *Hedyotis decumbens* Hochst.: *Krauss 305*, South Africa, Natal, MO 1801949. = *Oldenlandia affinis* (R. & S.) DC.

5. *Hedyotis globosa* Hochst. ex A. Rich.: *Schimper 512*, 20 Nov. 1839, Ethiopia, MO 1802020. = *Agathisanthemum globosum* (Hochst. ex A. Rich.) Klotzsch ex Hiern.

6. *Hedyotis monanthos* Hochst. ex A. Rich.: *Schimper 1370*, 30 July 1842, Ethiopia, MO 1801950. = *Oldenlandia monanthos* (Hochst. ex A. Rich.) Hiern.

7. *Hedyotis natalensis* Hochst.: *Krauss 86*, South Africa, Natal, MO 1801947. =*Conostomium natalense* (Hochst.) Bremek. var. *natalense*.

Ann. Missouri Bot. Gard. **52**(2): 212-213. 1965.

8. *Hedyotis pentamera* Hochst. ex Sond.: *Krauss* 332, South Africa, Natal, MO 1801945. = *Pentodon pentandrus* (Schum. & Thonn.) Vatke var. *minor* Bremek.

9. *Hedyotis pusilla* Hochst. ex A. Rich.: *Schimper 1522,* 26 Nov. 1842, Ethiopia, MO 1801935. = *Oldenlandia linearis* DC.

10. *Hedyotis schimperi* Presl: *Schimper 186 & 358,* 25 Apr. & 5 June 1835, Egypt, MO 1801927. =*Kohautia caespitosa* Schnizl. var. *schimperi* (Presl) Bremek. (type of variety).

11. *Knoxia senegalensis* Reichenb., nomen; *Kohautia senegalensis* Cham. & Schlecht., *Sieber 9,* Senegal, MO 1801930.

12. *Kohautia aphylla* Bremek.: *Dinter* 6679, 8 Sept. 1929, South West Africa, MO 1781811.

13. *Kohautia strumosa* Hochst., nomen; *Hedyotis strumosa* A. Rich.: *Kotschy 46,* 22 Sept. 1839, Sudan, MO 1801931. = *K. aspera* (Heyne ex Roth) Bremek.

14. *Kohautia thymifolia* Presl *a,* in sched.: *Drège s. n.,* South Africa, Natal, MO 1801939. = *K. lasiocarpa* Klotzsch var. *thymifolia* Bremek. (type of variety).

15. *Kohautia thymifolia* Presl *b,* in sched., Bremekamp (1952) in syn.: *Drège s. n.,* South Africa, Cape, MO 1801940. = *K. cynanchica* DC.

16. *Kohautia thymifolia* Presl *c,* in sched., Bremekamp (1952) in syn.: *Drège s. n.,* South Africa, Natal, MO 1802018. = *K. virgata* (Willd.) Bremek.

17. *Lelya osteocarpa* Bremek.: *Lely P96,* Jan. 1929, Nigeria, MO 1755946. = *L. prostrata* (R. Good) W. H. Lewis.

18. *Oldenlandia caffra* Eckl. & Zeyh.: *Eklon 2291,* South Africa, Cape, MO 1801956. = *Kohautia virgata* (Willd.) Bremek.

19. *Oldenlandia duemmeri* S. Moore: *Dümmer 2642,* Uganda, MO 1612608.

20. *Oldenlandia flosculosa* Hiern: *Hildebrandt 1348,* July 1874, Zanzibar, MO 1769965.

21. *Oldenlandia herbacea* (L.) Roxb. var. *suffruticosa* Bremek.: *Galpin 14929,* 23 July 1935, South Africa, Transvaal, MO 1766062 (type of variety).

22. *Oldenlandia kaessneri* S. Moore: *Kaessner 957,* 9 June 1902, Kenya, MO 1688276.

23. *Oldenlandia subtilis* S. Moore: *Kaessner 781,* Kenya, MO 1670172. = *Oldenlandia linearis* DC.

24. *Oldenlandia wiedemannii* K. Sch. var. *glabricaulis* Bremek.: *Kaessner* 653, 22 April 1902, Kenya, MO 1688275 (type of variety).

25. *Pentodon abyssinicus* Hochst.: *Schimper 1750,* Apr. 1839, Ethiopia, MO 1801946. = *P. pentandrus* (Schum. & Thonn.) Vatke var. *pentandrus.*

26. *Pentodon decumbens* Hochst.: *Krauss 332,* South Africa, Natal, MO 1801945. = *P. pentandrus* (Schum. & Thonn.) Vatke var. *minor* Bremek.

NEW COMBINATIONS IN NORTH AMERICAN CALYSTEGIA

By R. K. Brummitt

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As I have recently completed a revision of the genus *Calystegia*, Dr. W. H. Lewis and Mr. R. L. Oliver have invited me to publish the new combinations necessary for North American taxa simultaneously with their own paper dealing with the realignment of *Calystegia* and *Convolvulus*. Further details and discussion and descriptions of new taxa will be published in a full revision of the whole genus, at present being prepared for press. This work is taken largely from a thesis submitted for the degree of Ph.D. in the University of Liverpool in 1963, modified in the light of further research carried out at Kew.

In publishing this note I wish to record my indebtedness to Dr. S. M. Walters (Cambridge) and Professor D. A. Webb (Dublin) who investigated the Californian taxa some five years ago but avoided making new combinations until my own revision was complete. Their assistance and co-operation is gratefully acknowledged. I also wish to thank Dr. P. H. Raven for his most helpful discussion of some of the Californian taxa. Finally it is a pleasure to express my thanks to Dr. Lewis and Mr. Oliver and to record my complete agreement with the conclusions they have reached in their own paper.

Calystegia **purpurata** (Greene) Brummitt, comb. nov.

Basionym : *Convolvulus luteolus* A. Gray var. *purpuratus* Greene, Man. Bay Reg. Bot. 265. 1894.

subsp. **solanensis** (Jepson) Brummitt, comb. et stat. nov.

Basionym : *Convolvulus luteolus* A. Gray var. *solanensis* Jepson, Fl. W. Mid. Calif. 388. 1901.

subsp. **saxicola** (Eastwood) Brummitt, comb. nov.

Basionym : *Convolvulus saxicola* Eastwood, Bull. Torrey Bot. Club **30:** 495. 1903.

Calystegia **occidentalis** (A. Gray) Brummitt, comb. nov.

Basionym : *Convolvulus occidentalis* A. Gray, Proc. Amer. Acad. **11:** 89. 1876.

Calystegia **peirsonii** (Abrams) Brummitt, comb. nov.

Basionym : *Convolvulus peirsonii* (*'piersonii'*) Abrams, Ill. Fl. Pacific States **3:** 387. 1951.

Calystegia **longipes** (S. Watson) Brummitt, comb. nov.

Basionym : *Convolvulus longipes* S. Watson, Amer. Nat. **7:** 302. 1873.

Calystegia **macrostegia** (Greene) Brummitt, comb. nov.

Basionym : *Convolvulus macrostegius.* Greene, Bull. Calif. Acad. **1:** 208. 1885.

subsp. **cyclostegia** (House) Brummitt, comb. et stat. nov.

Basionym : *Convolvulus cyclostegius* House, Muhlenbergia **4:** 53. 1908.

subsp. **intermedia** (Abrams) Brummitt, comb. nov.

Ann. Missouri Bot. Gard. **52**(2): 214-216. 1965.

Basionym : *Convolvulus aridus* Greene subsp. *intermedius* Abrams, Contr. Dudley Herb. **3:** 357. 1946.

subsp. **longiloba** (Abrams) Brummitt, comb. nov.

Basionym : *Convolvulus aridus* Greene subsp. *longilobus* Abrams, Contr. Dudley Herb. **3:** 358. 1946.

subsp. **tenuifolia** (Abrams) Brummitt, comb. nov.

Basionym : *Convolvulus aridus* Greene subsp. *tenuifolius* Abrams, Contr. Dudley Herb. **3:** 359. 1946.

subsp. **arida** (Greene) Brummitt, comb. et stat. nov.

Basionym : *Convolvulus aridus* Greene, Pittonia **3:** 330. 1898.

Calystegia **fulcrata** (A. Gray) Brummitt, comb. nov.

Basionym : *Convolvulus luteolus* A. Gray var. *fulcratus* A. Gray, Proc. Amer. Acad. **11:** 90. 1876.

subsp. **gracilenta** (Greene) Brummitt, comb. et stat. nov.

Basionym : *Convolvulus gracilentus* Greene, Pittonia **3:** 329. 1898.

subsp. **tomentella** (Greene) Brummitt, comb. et stat. nov.

Basionym : *Convolvulus tomentellus* Greene, Pittonia **3:** 327. 1898.

var. **deltoidea** (Greene) Brummitt, comb. nov.

Basionym : *Convolvulus deltoideus* Greene, Pittonia **3:** 331. 1898.

subsp. **pedicellata** (Jepson) Brummitt, comb. nov.

Basionym : *Convolvulus malacophyllus* Greene var. *pedicellatus* Jepson, Fl. Calif. **3:** 121. 1939.

subsp. **malacophylla** (Greene) Brummitt, comb. et stat. nov.

Basionym : *Convolvulus malacophyllus* Greene, Pittonia **3:** 326. 1898.

Original description : *Calystegia villosa* Kellogg, Proc. Calif. Acad. **5:** 17. 1873, non Rafin., Fl. Ludov. 45. 1817, non *Convolvulus villosus* Pers., Syn. Pl. **1:** 177. 1805.

var. **berryi** (Eastwood) Brummitt, comb. nov.

Basionym : *Convolvulus berryi* Eastwood, Proc. Calif. Acad. ser. 3 Bot. **2:** 287. 1902.

Calystegia **collina** (Greene) Brummitt, comb. nov.

Basionym : *Convolvulus collinus* Greene, Pittonia **3:** 326. 1898.

subsp. **tridactylosa** (Eastwood) Brummitt, comb. et stat. nov.

Basionym : *Convolvulus tridactylosus* Eastwood, Proc. Calif. Acad. ser. 4, **20:** 151. 1931.

Calystegia **macounii** (Greene) Brummitt, comb. nov.

Basionym : *Convolvulus macounii* Greene, Pittonia **3:** 331. 1898.

Calystegia spithamaea (L.) Pursh, Fl. Am. Sept. **1:** 143. 1814.

subsp. **stans** (Michx.) Brummitt, comb. nov.

Basionym : *Convolvulus stans* Michx., Fl. Bor.-Am. **2:** 136. 1803.

subsp. **purshiana** (Wherry) Brummitt, comb. nov.

Basionym : *Convolvulus purshiana* Wherry, Proc. Pennsylv. Acad. Sci. **7:** 163. 1933.

Calystegia catesbeiana Pursh, Fl. Am. Sept. **2:** 729. 1814.
subsp. **sericata** (House) Brummitt, comb. et stat. nov.
Basionym : *Convolvulus sericatus* House, Torreya **6:** 150. 1906.

Calystegia sepium (L.) R. Br., Prodr. Fl. Nov. Holl. 483. 1810.
subsp. **binghamiae** (Greene) Brummitt, comb. et stat. nov.
Basionym : *Convolvulus binghamiae* Greene, Bull. Calif. Acad. **2:** 417. 1887.
subsp. **limnophila** (Greene) Brummitt, comb. et stat. nov.
Basionym : *Convolvulus limnophilus* Greene, Pittonia **3:** 329. 1898.
subsp. **americana** (Sims) Brummitt, stat. nov.
Basionym : *Convolvulus sepium* (L.) R. Br. var. *americanus* Sims, Bot. Mag. *t.* 732. 1804.

Calystegia **fraterniflora** (Mackenzie & Bush) Brummitt, comb. nov.
Basionym : *Convolvulus sepium* (L.) R. Br. var. *fraterniflorus* Mackenzie & Bush, Man. Fl. Jackson Co. Missouri 153. 1902.

REALIGNMENT OF CALYSTEGIA AND CONVOLVULUS (CONVOLVULACEAE)

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Since their separation by R. Brown (Prod. Fl. Nov. Holland 481. 1810), a majority of taxonomists have treated *Calystegia* and *Convolvulus* as distinct. One of the first to question this separation was Bentham (Fl. Austral. **4:** 428-431. 1868), who observed that *Calystegia* ". . . appears to be still too artificial to adopt . . . as a genus after Brown and others." He reduced *Calystegia* to a section of *Convolvulus* and also placed *Jacquemontia* in synonymy. Only eight years later, Bentham and Hooker (Gen. Plant. **2:** 874. 1876) reversed this treatment and recognized both *Calystegia and Jacquemontia.* In that year, Gray (Proc. Amer. Acad. **11:** 89-90. 1876) published his observations of certain Californian species in this complex and, strongly influenced by Bentham's original (but by then altered) conclusion, he considered *Calystegia* and *Convolvulus* as one. Subsequently, most species known to North America have been lumped under *Convolvulus,* while elsewhere the same and other species have been recognized by and large under either *Calystegia* or *Convolvulus.* Clearly this dichotomy should be resolved.

According to Hallier (Bot. Jahrb. **16:** 564, 579-580. 1893), species of *Calystegia* possess oblong or rarely filiform stigmas, incompletely 1-locular ovaries, and spherical pollen covered with pores, while those of *Convolvulus* have filiform stigmas, 2-locular ovaries, and ellipsoidal pollen with three longitudinal furrows. O'Donell (Lilloa **29:** 299-311. 1959) separated the genera on much the same basis, namely, that *Calystegia* species are characterized by flat and oblong stigmas, semilocular ovaries, large bracts and spheroidal pollen having many evenly distributed pores, while species of *Convolvulus* differ by having cylindrical and pointed stigmas, bilocular ovaries, reduced bracts and ellipsoidal pollen with three furrows and three pores. In a family notorious for few characters distinguishing recognized genera, these would appear ample if in fact they were correct and without exception.

Because the morphology of the pollen was emphasized by the above workers and because their descriptions differed, i.e. Hallier (loc. cit.) reported the pollen of species of *Convolvulus* as 3-colpate and O'Donell (loc. cit.) as 3-colporate, our study began with an investigation of the male gametophyte. Our experience with members of other families led us to discount the pessimism expressed by Kuntze (Rev. Gen. **3:** 209-211. 1899), Roberty (Candollea **14:** 19. 1952) and MacBride (Field Mus. Nat. Hist., Bot. ser., **13**(5): 481. 1959) who noted that pollen characteristics of members of the *Convolvulaceae* are inconsistent and as such are scarcely usable in unravelling complex problems. Anthers were removed from herbarium specimens and pollen grains were acetolyzed and mounted for perma-

Ann. Missouri Bot. Gard. **52**(2): 217-222. 1965.

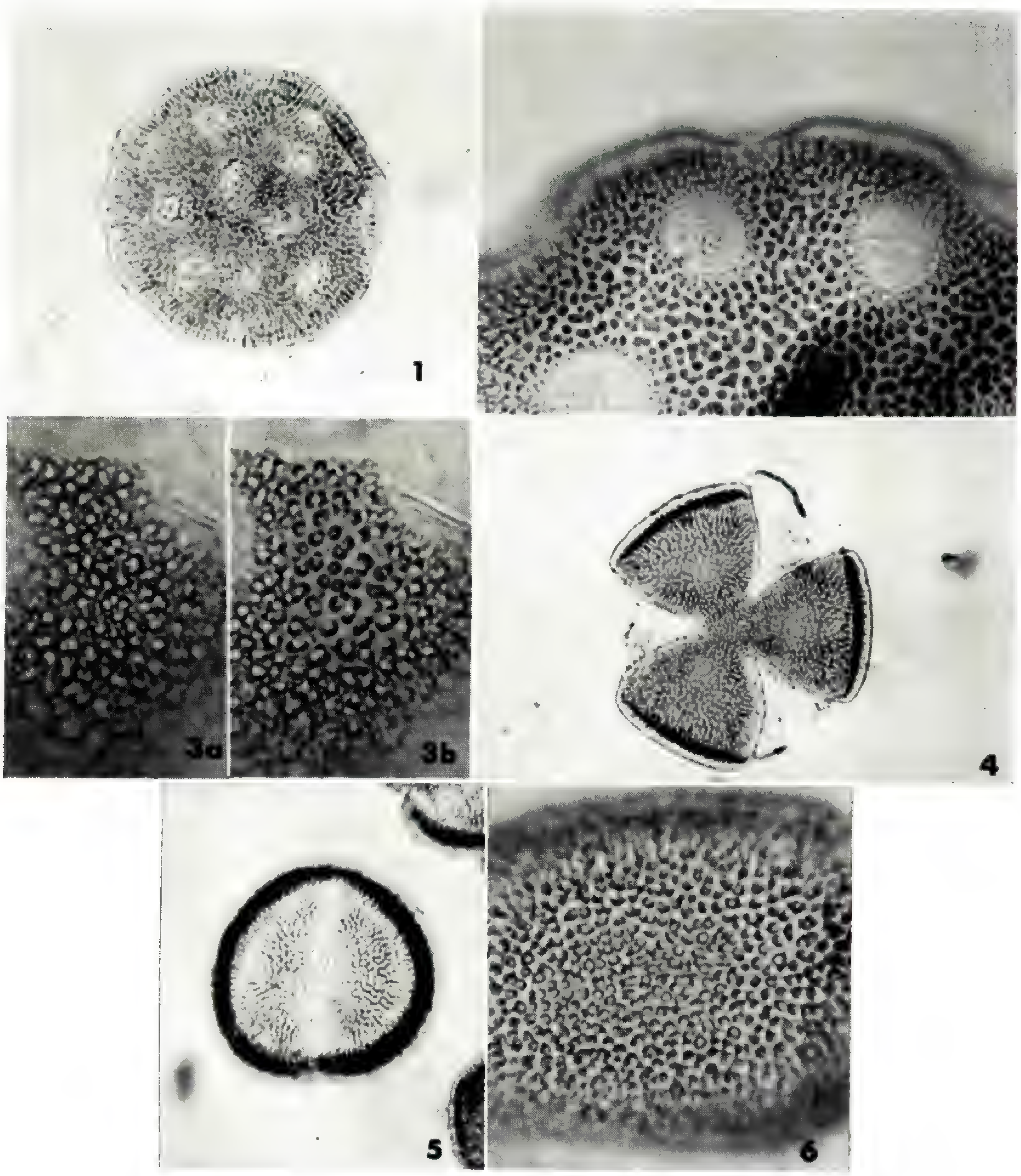

Fig. 1-6. Pollen grains of *Calystegia* and *Convolvulus*. Fig. 1. Whole grain of *Calystegia pulchra* Brummitt & Heywood (*Brummitt s. n.*), × 320. Fig. 2. Wall segment of *Calystegia occidentalis* (Gray) Brummitt (*Hammond 302*) focused on the endosexine showing bacula and pores, × 800. Fig. 3. Curved wall segment of *Calystegia macrostegia* (Greene) Brummitt (*Trask 54*) at two focuses showing (a) punctitegillate ectosexine (dark puncta at uppermost focus, light puncta at lower focus) and (b) infrategillar bacula of endosexine at lowest focus, × 1070. Fig. 4-6. Whole grains and a wall segment of *Convolvulus althaeoides* L. (*Cook 345*). Fig. 4. Polar view showing much extended colpi and remains of membranes, × 320. Fig. 5. Equatorial view showing one colpus, × 320. Fig. 6. Infrategillar bacula of endosexine, × 800.

nent reference by the procedures outlined by Erdtman (Pollen morphology and plant taxonomy. Angiosperms. 1952).

Pollen from 83 collections representing 60 taxa separated into two groups with remarkably little difference between the grains of each group. Their characteristics did not change with maturity, nor did they differ from individual to individual within the same species. Pollen grains of the first group (Fig. 1-3) which includes *C. sepium* (L.) R. Br., the type species of *Calystegia,* and 24 additional taxa listed in Appendix 1 are large (at maturity ca. 60-95μ in diameter) and spheroidal or rarely suboblate. The apertures are simple, numerous (ca. 20-40 per grain) and pantoporate (forate), the pores 3μ × 5μ to 6μ × 9μ, usually ovate and somewhat irregular in outline with a membrane bearing numerous excrescences to 2.5μ in diameter. The sexine midway between the pores is 3-4.5μ in thickness, reducing markedly toward the pores, and consisting of a thin (ca. 1μ), punctitegillate ectosexine, L-O pattern, and a thicker endosexine of infrategillar, often branched bacula. These bacula are scattered, usually irregular in outline and to ca. 2.5μ in diameter. The nexine is 1.0-1.7μ in thickness. Pollen grains of the second group (Fig. 4-6) which includes *C. arvensis* L., the type species of *Convolvulus,* and 39 additional taxa listed in Appendix 1 are medium to large (at maturity 44μ (E) × 33μ (P) to 75μ × 62μ) and prolate to more frequently subspheroidal. The apertures are simple, 3 or rarely 4 per grain and zonocolpate, the colpi long (ca. 30-40μ) and narrow (ca. 3-4μ), somewhat longer and often much broader at the time of pollen shedding with a membrane covered with numerous small excrescences. The sexine is 2.2-3.5μ in thickness, consisting of a thin (to 1μ), punctitegillate ectosexine, L-O pattern, and a thicker endosexine similar to that described for pollen of *Calystegia.* The nexine is 1.0-1.5μ in thickness.

Pollen grains typical of *Calystegia* are readily identified by their spheroidal shape and many pantoporate apertures per grain. This morphology is rare among pollen of 33 other convolvulaceous genera examined and is known only for *Merremia tridentata* (L.) Hall. f. and several species of *Prevostea.* Pollen grains of all species of *Convolvulus* are distinguished from those of *Calystegia* by their prolate to subspheroidal shapes and the 3-(4-) zonocolpate apertures per grain with distinct polar and equatorial axes. This form is common to the greatest number of genera in the family. It agrees with Hallier's (Bot. Jahrb. **16:** 564, 579-580. 1893) description of the aperture, but not with that of O'Donell (Lilloa **29:** 299-311. 1959) who incorrectly recognized a complex colpus plus os morphology for *Convolvulus.*

The divergence in pollen morphology between the two genera is so great that most palynologists would consider the two only distantly related. Sporophytic differences, however, are not so great and many competent North American taxonomists would consider them congeneric. Is this an example of convergence only of the sporophytic part of the generations while male gametophytes evolved along divergent pathways? Yet there are some differences between the sporophytes of these genera. On examining the stigmas for all taxa listed in Appendix 1 we found that the sporophytes separated into two groups corresponding exactly to the two palynological groupings identified as *Calystegia* and *Convolvulus.* For species of *Caly-*

stegia the paired stigmas are oblong, (2)-3-(4) times as long as broad, ± cylindrical, with blunt apices and a demarcation between the stigmatic areas and the style (Fig. 7-9 from herbarium specimens). For those of *Convolvulus* the paired stigmas are linear or linear-spatulate, ± applanate, with acutate apices and without a distinct separation between the stigmatic area and the style (Fig. 10-12 from herbarium specimens). The stigmas of a few species of *Convolvulus* may vary,

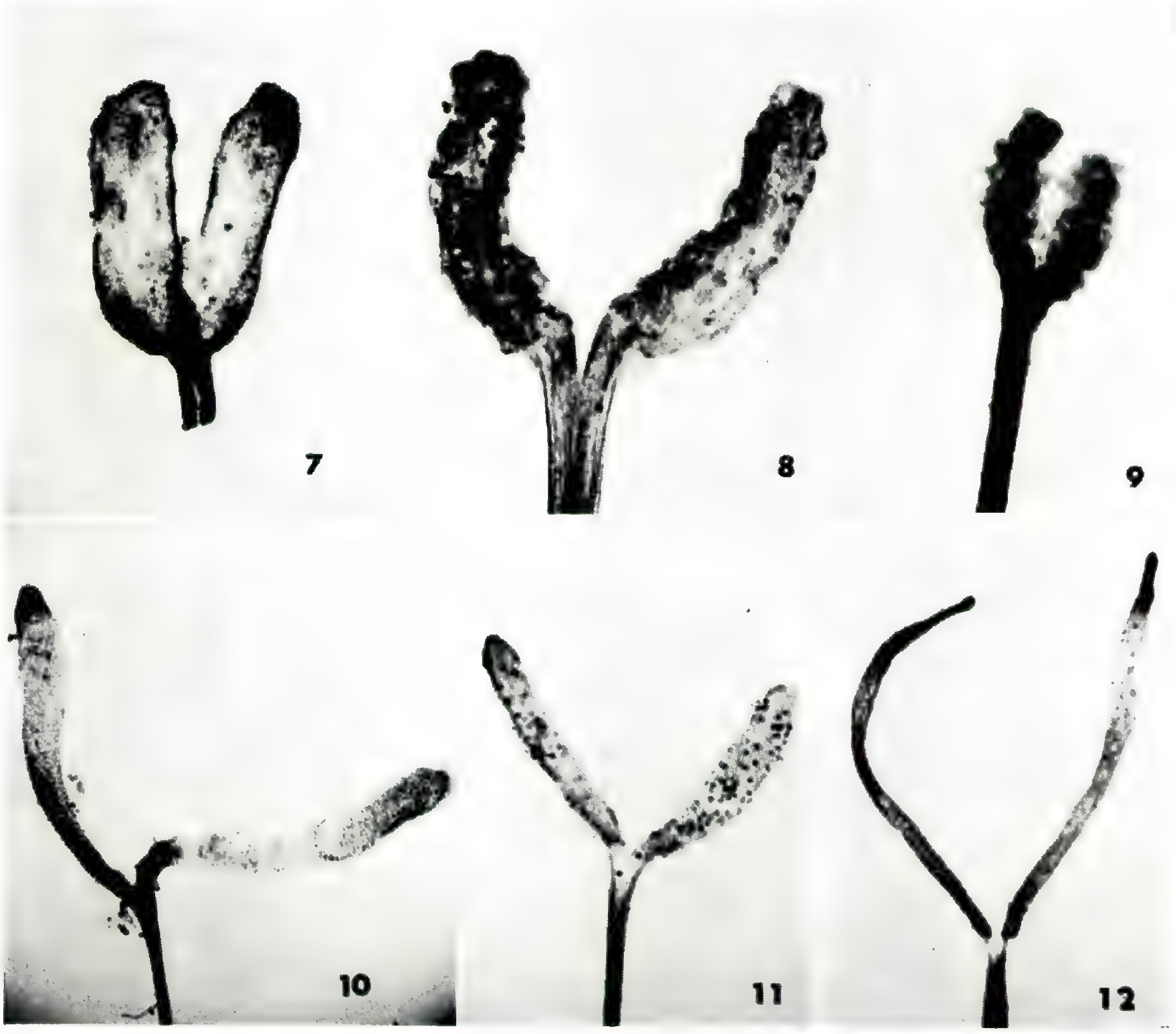

Fig. 7-12. Stigmas and parts of styles of *Calystegia* and *Convolvulus*. × 10. Fig. 7. *Calystegia macrostegia* subsp. *cyclostegia* (House) Brummitt, *Anthony 206*. Fig. 8. *C. sepium* (L.) R. Br., *Drones 1546*. Fig. 9. *C. soldanella* (L.) R. Br., *Charette 1685*. Fig. 10. *Convolvulus arvensis* L., *Trelease 611*. Fig. 11. *C. arvensis* L. (as *C. sagittifolius* Fisch ex Choisy), *Dorsett & Dorsett 3361*. Fig. 12. *C. floridus* L. f., *Bornmüller 2616*.

e.g. in *C. dissectus* these are short and broad, but flattened, and their apices are acutate and thereby closely resemble those of typical members of this large genus.

Since most herbarium specimens bear flowers, there is no difficulty in separating the species on the basis of stigmatic differences, but the specimens represented solely by fruit require an additional character for generic determination. The septum of members of *Calystegia* is incomplete and may be so reduced that it is barely discernible at the edge of the pericarp. Although fruit was not available for all species otherwise examined, the unilocular ovary was typical of all species of *Calystegia*

found in North America. In contrast, all species of *Convolvulus* represented in North America have fruit with complete septa and these are 2-locular.

Other sporophytic characters which may be of use in distinguishing the genera are the position and kind of floral bracts and the numbers of flowers per inflorescence. Bracts of many species of *Calystegia* enclose or closely subtend the calyx and they are large and sepal-like, while the bracts of most species of *Convolvulus* are much smaller, leaf-like and do not closely subtend the calyx. Exceptions are known for both genera, however, and the bracts of *Calystegia purpurata* and *C. longipes*, and to a lesser extent *C. occidentalis* and *C. peirsonii*, resemble those of many species of *Convolvulus*. On the other hand, the bracts of *Convolvulus gharbensis*, *C. jeffreyi*, *C. undulatus* and others, closely approximate those known for a majority of the species of *Calystegia*. A second difference is seen in the inflorescences: species of *Calystegia* usually have solitary flowers, those of *Convolvulus* often have inflorescences with many flowers. Since some individuals in each genus vary and some species typically have the expression common to the other genus these are trends only, and together with the characteristics of the floral bracts they are of limited diagnostic value in distinguishing *Calystegia* and *Convolvulus*.

In summary, the species of *Calystegia* and *Convolvulus* are distinguished by the following criteria.

	Calystegia	*Convolvulus*
MALE GAMETOPHYTE:		
shape	spheroidal	prolate to subspheroidal
aperture number	about 20 to 40	3, rarely 4
aperture position	pantotreme	zonotreme
aperture kind	porate	colpate
sexine	undulating in thickness	± even in thickness
SPOROPHYTE:		
stigma	oblong, ± cylindrical, apices blunt, stigmatic area and style distinct	linear, ± applanate, apices acutate, stigmatic area and style ± continuous; very rarely short and spatulate, but then applanate with acutate apices
fruit (N. Am. species)	1-locular, septum incomplete	2-locular, septum complete

Appendix 1

The following is a list of species studied palynologically, giving the collector and number and the state (U. S.) or country of collection (all MO). Under *Calystegia* we have endeavored to follow Dr. R. K. Brummitt's new combinations (cf. this issue, p. 214) which he most generously has made available at this time.

Calystegia atriplicifolia Hall f., *Schoth s. n.* (Oregon); C. *collina* (Greene) Brummitt, *Baker 2968* (California); *C. fraterniflora* (Mackenzie & Bush) Brummitt, *Jones 16469* (Illinois), *Palmer 3451* (Missouri); *C. fulcrata* (Gray) Brummitt subsp. *gracilenta* (Greene) Brummitt, *Wolf 8036* (California); *C. fulcrata* subsp. *malacophylla* (Greene) Brummitt,

Heller 13280 (California); *C. fulcrata* subsp. *malacophylla* var. *berryi* (Eastw.) Brummitt, unknown collector, Fink Herb. (California); *C. fulcrata* subsp. *pedicellata* (Jepson) Brummitt, *Wolf 6893* (California); *C. hederacea* Wall., *Okamoto* NSM 538 (Japan); *C. japonica* Choisy, *Charette 1846* (Japan); *C. longipes* (S. Wats.) Brummitt, *Duran 3468* (California); *C. macounii* (Greene) Brummitt, *Bush 1998* (Missouri), *Morrison 1082* (*Convolvulus interior* House) (Nebraska); *C. macrostegia* (Greene) Brummitt, *Trask 54* (California); *C. macrostegia* subsp. *arida* (Greene) Brummitt, *Parish 4153* (California); *C. macrostegia* subsp. *cyclostegia* (House) Brummitt, *Angier 58* (California), *Eastwood 219* (California); *C. marginata* R. Br., *Matthews 171* (New Zealand); *C. occidentalis* (Gray) Brummitt, *Hammond 302* (Oregon), *Heller 13202* (California), *Wolf 8656* (California), *Copeland 674* (*Convolvulus polymorphus* Greene) (California); *C. pulchra* Brummitt & Heywood, *Brummitt s. n.* (England); *C. sepium* (L.) R. Br., *Cronquist 4339* (Georgia); *C. sepium* subsp. *americana* (Sims) Brummitt, *Drones 1546* (Massachusetts); *C. sericata* (House) Bell, *House 28167* (cult. New York); *C. silvatica* (Kit.) Griseb., *Schneider 515* (*Bulgaria*), *? van Schrenk s. n.* (New York); *C. soldanella* (L.) R. Br., *Charette 1685* (Japan), *Otis 2104* (Washington); *C. spithamaea* (L.) Pursh, *Bissell 149* (Connecticut), *Eggert s. n.* (Missouri), *Lakela 2953* (Minnesota); *C. subacaulis* Hook. &. Arn., *Baker 848* (California); *C. tuguriorum* (G. Forster) Hook., *Matthews 1709* (New Zealand).

Convolvulus althaeoides L., *Rechinger 16173* (Greece), *Cook 345* (Canary I.); *C. ammannii* Desr., *Maltzev 3764a* (U. S. S. R.), *Reverdatto 3764b* (U. S. S. R.); *C. arvensis* L., *Dorsett & Dorsett 3361* (Manchuria), *Malme 2936* (Argentina); *C. canariensis* L., *Pitard 257* (Canary I.); *C. cantabrica* L., *Berza 68* (Rumania); *C. crenatifolius* Ruiz & Pav., *Mosén 4291* (Brazil); *C. dorycnium* L., *Baldacci 137* (Greece); *C. equitans* Benth., *Demaree 13291* (Oklahoma), *Tharp s. n.* (*C. hermannioides* A. Gray) (Texas), *Wynd & Mueller 74* (Mexico); *C. erinaceus* Ledeb., *Granitov 442* (U S. S. R.); *C. erubescens* Sims, *von Mueller s. n.* (Australia); *C. farinosus* L., *Pillans 10370* (S. Africa); *C. floridus* L. f., *Bornmüller 2616* (Canary I.); *C. fruticosus* Pall., *Androssov 3768a* (U. S. S. R.); *C. gharbensis* Battand & Pitard, *Romieux 1388* (Morocco); *C. hirsutus* Bieb., *Haradjian 729* (Cyprus); *C. incanus* Vahl, *Wagenknecht 18445, 18462* (Chile); *C. jeffreyi* Verdc., *Tanner 2211* (Tanganyika); *C. kilimandschari* Engl., *Verdcourt 1207* (Tanganyika), *Schleiben 4343* (Tanganyika); *C. laciniatus* Desr., *Gallinal et al. B-197* (Uruguay); *C. lineatus* L., *Schiraevsky 3770b* (U. S. S. R.); *C. mollis* Meissn., *Dusén 15683* (Brazil); *C. montanus* van Ooststr., *Vargas 3052* (Peru); *C. montevidensis* Spreng., *Mexia 4351* (Argentina); *C. natalensis* Bernh., *Strey 3460* (S. Africa); **C. nodiflorus* Desr., *Heller 6060* (Puerto Rico), *Otero 292* (Puerto Rico); *C. oleaefolius* Desr., *Pampanini 6215* (Libya); *C. ottonis* Meissn., *Dusén 1303a* (Brazil); *C. oxyphyllus* Boiss., *Barkley & Andrew 2407* (Iraq); *C. pilosellaefolius* Desr., *Rechinger & Rechinger 3617* (Iran); *C. pluricaulis* Choisy, *Dudgeon s. n.* (India); *C. pseudo-cantabrica* Schrenk, *Mokeeva & Popov 154* (U. S. S. R.); *C. scammonia* L., Kellogg *s. n.* ("Asia Minor"); *C. siculus* L., *Norton s. n.* (cult. M. B. G.); *C. simulans* L. M. Perry, *Dressler 670* (Mexico); *C. subhirsutus* Regel & Schmalh., *Vvedensky 444* (U. S. S. R.); *C. suffruticosus* Desf. var. *oranensis* Pom., *Faure s. n.* (Morocco); *C. tenuissimus* Sibth. & Sm., *Mayer s. n.* (Yugoslavia); *C. tricolor* L., *Thompson 148* (cult. M. B. G.); *C. undulatus* Cav., *Reverschon 295* (Algeria); *C. virgatus* Boiss., *Rechinger & Rechinger 3988* (Iran).

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* MacBride (Field Mus. Nat. Hist., Bot. ser., **13**(5): 512, 518. 1959) included *C. nodiflorus* in *Jacquemontia* while noting that it better fits *Convolvulus.* The pollen of *Jacquemontia* species is distinct from pollen of *Convolvulus* and this species must be included in the latter.

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VOLUME LII

No. 3

Annals of the Missouri Botanical Garden

ROBERT E. WOODSON, JR. MEMORIAL ISSUE

September, 1965

PUBLISHED QUARTERLY BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN
AND WASHINGTON UNIVERSITY PRESS
ST. LOUIS, MISSOURI

Annals
of the
Missouri Botanical Garden

A quarterly journal containing scientific contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

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THE ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Beginning with Volume 45, 1958:

Subscription Price	$15.00 per volume
Single Numbers	4.00 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Beginning June 1, 1962 the Stechert-Hafner Service Agency, Inc., 31 East 10th St., New York 3, N. Y., became sole agent for the ANNALS OF THE MISSOURI BOTANICAL GARDEN. The Agency handles all subscriptions, all claims beginning with volume 50 (1963) and all requests for back issues. Out-of-print numbers will be reprinted as may be required.

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Annals
of the
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Vol. LII — September, 1965 — No. 3

ROBERT E. WOODSON, JR. MEMORIAL ISSUE

On behalf of the Director and the Board of Trustees of the Missouri Botanical Garden, we take pleasure in dedicating this Issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN to the late Dr. Robert E. Woodson, Jr. We appreciate the enthusiastic response from among his many colleagues and friends for their contributions.

EDITORIAL COMMITTEE
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The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. **52,** No. 2, pp. 99-222, was published on July 27, 1965.

Dr. Robert E. Woodson, Jr., at the age of 22.
Photograph courtesy Miss Roberta Woodson.

ROBERT E. WOODSON, JR. (1904-1963)

By Mildred E. Mathias

Department of Botany, University of California, Los Angeles

Woodson, Prof. Robert E(verard), Jr., Dept. of Botany, Washington University, St. Louis 5, Mo. Botany. St. Louis, Mo. April 28, 04. A.B., Washington (St. Louis), 26, M. S, 27, Ph.D(bot), 29; Lackland fel, Mo. Bot. Garden, 26-27, 28-29; A. M. Harvard, 28. Instr. Bot, Washington (St. Louis), 29-35, asst. prof, 35-42, Assoc. prof, 42-45, Prof, 45-; Curator Herbarium, Mo. Bot. Garden, 58-, asst, 29-37, asst. curator herbarium, 37-47, curator 48-55. Consult, Ciba Pharmaceut. Prods, Inc, 53-Soc. Plant Taxon. (sec-treas, 47; pres, 53); Bot. Soc; Soc. Study Evolution. Plant taxonomy; evolution.

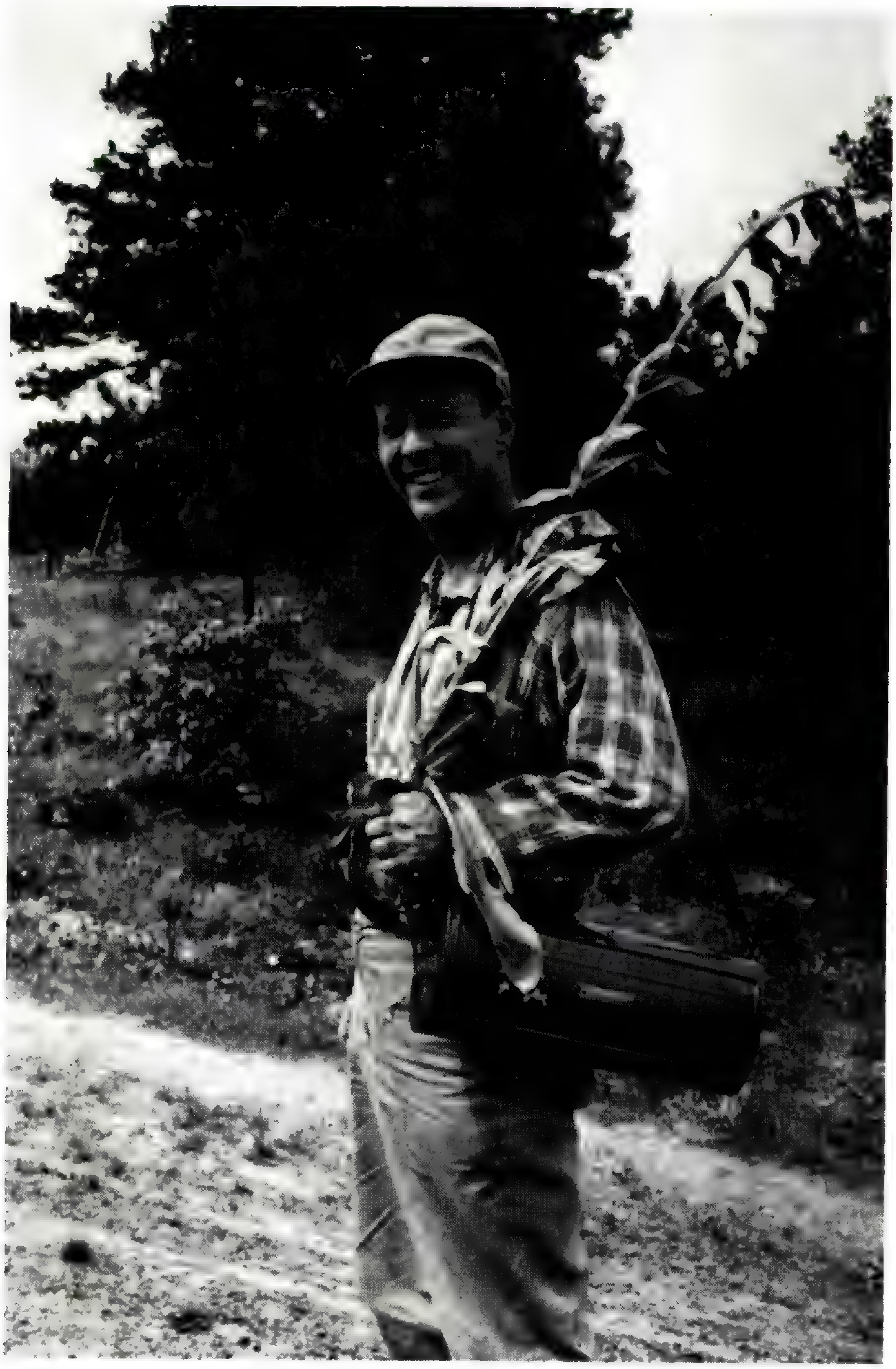
This concise abbreviated biography from the tenth edition of American Men of Science can now be completed: Died, St. Louis, Mo. Nov. 6, 1963. Too often we know our colleagues from such dry as bone vital statstics which give us no insight into the real individuals. Bob Woodson was unique, like his mentors a gentleman of the old school, almost Victorian in many ways, yet with a keen interest in students and teaching, and with an insatiable curiosity about the world around him. It is difficult to add to the sensitive biographical notes recently published by Allen, Caroline K., David J. Rogers, & Lorin I. Nevling, Jr. in Brittonia **17:** 1-11. 1965, but the following reminiscences may give some insight into a many-faceted personality.

I first met Bob as a classmate at Washington University, St. Louis, in the days when undergraduate botany was taught in a World War I "temporary" building beside the streetcar tracks. We were two of a close-knit group of four botany majors spending all of our free hours in the laboratory together. It was here that Bob started an herbarium collection to which we contributed and which eventually reached a size where printed labels were needed. This was the beginning of a long series of anecdotes for the printer's bill arrived addressed to "Mr. Herb. Robert E. Woodson, Jr." and from there on Bob was sometimes familiarly known botanically as Herb Robert.

Our senior year took us to the Missouri Botanical Garden for lectures and laboratories conducted by Jesse More Greenman, Edgar Anderson, and George T. Moore, and introduced us to a broadened horizon not only of botany but literature for we discovered a delightful way of "waiting" for class by exploring Henry Shaw's personal library then relegated to the far corners of a basement room. Here we read aloud from the "Arabian Nights" and other treasures and enjoyed the fine old worn leather bindings along with the dust of years.

It was about this time that Bob acquired his first automobile, a great improvement in our collecting transportation since we had been confined to areas reached by the streetcars. One of our favorites had been the Creve Coeur Lake line, where

Ann. Missouri Bot. Gard. **52**(3): 225-228. 1965.



Dr. Woodson on field trip in Missouri during the summer of 1959.

at the lake terminus we became acquainted with the ferns and mosses and my copy of Grout's "Mosses with a Hand Lens" got intensive use. The new automobile further broadened our horizons and we travelled far in search of plants in Paris Green, for all cars must have names. Shortly Paris Green was followed by Bucephalus, a real winged horse, which took us flying to Pickle Springs and the St. Francis River Shut-ins. By now we had moved into graduate school and Bob acquired yet another name with the organization of the Klutz Family. He was christened Valentine, a name most appropriate for this blond handsome youth.

But there is still another set of names. One summer while I was away I re-

Dr. Woodson in the Library of the Missouri Botanical Garden examining folios with Mr. George Freytag.

ceived a series of three postcards from Bob, the first "From hypogyny," followed by "Through perigyny," and then naturally "To epigyny," each illustrated with a sketch of a small girl with pigtails, starting in the normal position for such appendages and being raised erect and closely appressed above the top of the head in the last communication.

Interspersed with hard work, much study, curatorial duties in the herbarium, and field trips were the occasional graduate student parties, often at the Anderson's, where one of the treats was beaten biscuits which we beat by running the dough through a hand clothes wringer as Bob's Virginia relatives had taught him.

Perhaps this set of random memories will give you an insight into the whimsical, enthusiastic student of natural history who was shortly to move on to Harvard University for more experiences. There he fell under the spell of Professor E. C. Jeffrey and the study of anatomy. This interest was to continue throughout his life and resulted in the development of a course which he taught for many years. It also influenced the publications of Woodson and his students. From Harvard Bob returned to the Missouri Botanical Garden to complete the Ph.D. and to join the staff of the Garden and the University, a position which he held for his entire career. Here he continued his studies of the *Apocynaceae* and *Asclepiadaceae* and

launched the Flora of Panama project with a series of expeditions to Panama. When the travel restrictions of World War II made field work difficult he initiated the study of *Asclepias tuberosa* which led to a series of papers which are already classics in their presentation and analysis of data.

In the decade before his death he was deeply involved in the investigation on *Rauwolfia* as a consultant for Ciba. This led to an interest in the drug potentials of American *Apocynaceae* and the collection of specimens by Felix Woytkowski in the Peruvian Amazon. Bob's encouragement of Woytkowski and their active correspondence has produced an impressive herbarium collection of Peruvian plants now on file at the Missouri Botanical Garden.

Although Bob did not often participate in large scientific meetings the Garden was a regular stop for his taxonomic peers and a gathering place for many students. He was long a member of the Council of the American Society of Plant Taxonomists and one of its presidents. His advice and counsel were sought by many and his critical observations valued. An hour in his office surrounded by specimens and manuscripts and refreshed by the inevitable bottle of Coca-Cola was a memorable experience. It was on such a visit that I last saw Bob and his words to me as I left his office were "Don't believe everything Valentine says," a statement which could be a motto for the critical.

A CATALOGUE OF THE PUBLISHED WORKS OF ROBERT E. WOODSON, JR.

COMPILED BY LORIN I. NEVLING, JR.

Arnold Arboretum and Gray Herbarium, Harvard University, Cambridge, Massachusetts

A chronologically arranged bibliography of Robert E. Woodson, Jr., was published in Brittonia **17:** 6-11. 1965. This is a reprint of that list excluding the references to the Flora of Panama series.[1] Following the bibliography is a finding list arranged according to the major fields of his interests.

1925

1. The quest of the mandrake. Missouri Bot. Gard. Bull. **13:** 151-156, *pls.* 38, 39.

1926

2. The doctrine of signatures. Missouri Bot. Gard. Bull. **14:** 97-102, *pl.* 32.

1928

3. *Dysosma*: a new genus of *Berberidaceae*. Ann. Missouri Bot. Gard. **15:** 335-340, *pl. 46.*
4. Studies in the *Apocynaceae*. II. A revision of the genus *Stemmadenia*. Ann. Missouri Bot. Gard. **15:** 341-378.
5. Studies in the *Apocynaceae*. III. A monograph of the genus *Amsonia*. Ann. Missouri Bot. Gard. **15:** 379-434.

1929

6. Studies in the *Apocynaceae*. IIIA. A new species of *Amsonia* from the South-Central States. Ann. Missouri Bot. Gard. **16:** 407-410.

1930

7. The dogbane: roadside weed and future staple. Missouri Bot. Gard. Bull. **18:** 87-104, *pls. 14-18.*
8. Studies in the *Apocynaceae*. I. A critical study of the *Apocynoideae* (with special reference to the genus *Apocynum*). Ann. Missouri Bot. Gard. **17:** 1-213.

1931

9. *Apocynaceae*. *In* GLEASON, H. A. Botanical results of the Tyler-Duida expedition. Bull. Torrey Bot. Club **58:** 452-454.
10. New or otherwise noteworthy *Apocynaceae* of tropical America. Ann. Missouri Bot. Gard. **18:** 541-556.
11. New South American *Asclepiadaceae*. Ann. Missouri Bot. Gard. **18:** 557-563.
12. Vegetable Marble. Missouri Bot. Gard. Bull. **19:** 142, 143.

1932

13. The identity and nomenclature of *Apocynum androsaemifolium* L. Rhodora **34:** 30, 31.
14. The most interesting tree in Missouri. Missouri Bot. Gard. Bull. **20:** 145-149.
15. New or otherwise noteworthy *Apocynaceae* of tropical America. II. Ann. Missouri Bot. Gard. **19:** 45-76.
16. New or otherwise noteworthy *Apocynaceae* of tropical America. III. Ann. Missouri Bot. Gard. **19:** 375-387.

1933

17. A new yellow *Nymphaea* from tropical Africa (with G. H. PRING). Ann. Missouri Bot. Gard. **20:** 1-7.
18. *Apocynaceae*. *In* GLEASON, H. A., and A. C. SMITH. Plantae Krukovianae. Bull. Torrey Bot. Club **60:** 392.
19. Studies in the *Apocynaceae*. IV. The American genera of *Echitoideae* (see also 1935, 1936). Ann. Missouri Bot. Gard. **20:** 605-790.

[1]For an index to the Contributions toward a Flora of Panama and to the Flora of Panama, see article compiled by Dr. André Robyns beginning on page 234 of this issue.

ANN. MISSOURI BOT. GARD. **52**(3): 229-233. 1965.

1934

20. *Apocynaceae. In* Cufodontis, G. Risultati della spedizione biologica Austriaca in Costarica nel 1930. Arch. Bot. Forli **10:** 38-41.
21. *Apocynaceae* and *Asclepiadaceae. In* Rehder, A. Notes on the ligneous plants described by Léveillé from eastern Asia. J. Arnold Arb. **15:** 310-318.
22. New or otherwise noteworthy *Apocynaceae* of tropical America. IV. Ann. Missouri Bot. Gard. **21:** 613-623.
23. Two new asclepiads from Szechuan, China. Ann. Missouri Bot. Gard. **21:** 609-611.

1935

24. *Apocynaceae. In* Cufodontis, G. La piante raccolte durante la specizione biologica Austriaca in Costarica nel 1930. Arch. Bot. Forli **11:** 178, 179.
25. The floral anatomy and probable affinities of the genus *Grisebachiella.* Bull. Torrey Bot. Club **62:** 471-478.
26. New *Apocynaceae* and *Asclepiadaceae.* Collected by the expedition of the University of Michigan to the State of Tamaulipas, Mexico (1930), and the joint expeditions of the University of Michigan and the Carnegie Institution of Washington to Guatemala (1931) and the Yucatan Peninsula (1932). Am. J. Bot. **22:** 684-693.
27. Observations on the inflorescence of *Apocynaceae* (with special reference to the American genera of *Echitoideae*). Ann. Missouri Bot. Gard. **22:** 1-48, *pl.* 3.
28. On the occurrence of *Lacmellea* and a new species of *Zschokkea* in Central America. Tropical Woods **44:** 22-24.
29. The species of *Tradescantia* indigenous to the United States (with E. Anderson). Contr. Arnold Arb. **9:** 1-132, *pls. I-XII.*
30. Studies in the *Apocynaceae.* IV. The American genera of *Echitoideae* (continuation, see also 1936). Ann. Missouri Bot. Gard. **22:** 153-306.
31. *Temnadenia. In* Lemée, A. Dictionnaire descriptif synonymique des genres de plantes Phanerogames **6:** 480, 481.
32. *Tradescantia Wrightii* in New Mexico (with L. Hubricht). Rhodora **37:** 454, 455.

1936

33. Additions to the genus *Amsonia.* Bull. Torrey Bot. Club **63:** 35, 36.
34. Observations on the floral fibres of certain *Gentianaceae.* Ann. Bot. **50:** 759-766, *pls. 15, 16.*
35. Studies in the *Apocynaceae.* IV. The American genera of *Echitoideae* (concluded). Ann. Missouri Bot. Gard. **23:** 169-439.
36. Studies in the *Apocynaceae.* V. A revision of the Asiatic species of *Trachelospermum* Lem. Sunyatsenia **3:** 65-105.
37. Studies in the *Apocynaceae.* VI. *Kibatalia* and its immediate generic affinities. Philippine J. Sci. **60:** 205-229, *pl. 1.*

1937

38. A Laboratory Introduction to General Plant Biology (with M. Maxine Larisey). 97 pp., *50 pls.* St. Louis.
39. New or otherwise noteworthy *Apocynaceae* of tropical America. V. Ann. Missouri Bot. Gard. **24:** 11-16.

1938

40. *Apocynaceae. In* North American Flora **29:** 103-192.
41. Studies in the *Apocynaceae.* VII. An evaluation of the genera *Plumeria* L. and *Himatanthus* Willd. Ann. Missouri Bot. Gard. **25:** 189-224.
42. The vascular anatomy and comparative morphology of apocynaceous flowers (with J. A. Moore). Bull. Torrey Bot. Club **65:** 135-166. *pls. 1-5.*

1939

43. *Apocynaceae. In* Gleason, H. A., and E. P. Killip. The flora of Mount Auyan-Tepui, Venezuela. Brittonia **3:** 190.
44. *Apocynaceae* and *Asclepiadaceae. In* Smith, A. C. Notes on a collection of plants from British Guiana. Lloydia **2:** 207-209.
45. New or otherwise noteworthy *Apocynaceae* of tropical America. VI. Ann. Missouri Bot. Gard. **26:** 95-98.

46. New or otherwise noteworthy *Apocynaceae* of tropical America. VII. Ann. Missouri Bot. Gard. **26**: 257-259.
47. Two new asclepiads from the western United States. Ann. Missouri Bot. Gard. **26**: 261-264.
48. *Zingiberaceae. In* SMITH, A. C. Notes on a collection of plants from British Guiana. Lloydia **2**: 171, 172.

1940

49. Apocynaceae. *In* SMITH, A. C. *et al.* A collection of flowering plants from Mount Roraima and adjacent Venezuela, British Guiana, and Brazil. Bull. Torrey Bot. Club **67**: 298.
50. The apocynaceous flora of the Yucatan Peninsula. *In* LUNDELL C. L. Botany of the Maya Area. XV. Carnegie Inst. Washington Publ. **522**: 59-102.
51. Una nueva especie santafecina de "*Rhabdadenia.*" Lilloa **5**: 199, 200.

1941

52. Miscellaneous new *Asclepiadaceae* and *Apocynaceae* from tropical America. Ann. Missouri Bot. Gard. **28**: 271-286.
53. The North American *Asclepiadaceae.* I. Perspective of the genera. Ann. Missouri Bot. Gard. **28**: 193-244.
54. Two new asclepiads from the southwestern United States (with B. MAGUIRE). Ann. Missouri Bot. Gard. **28**: 245-248.

1942

55. Commentary on the North American genera of *Commelinaceae.* Ann. Missouri Bot. Gard. **98**: 141-154.
56. Plants to meet the war emergency. Rubber. Missouri Bot. Gard. Bull. **30**: 113-120.

1943

57. A new *Amsonia* from the Ozarks of Arkansas. Rhodora **45**: 328, 329.

1944

58. *Apocynaceae. In* MOLDENKE, H. N. Contributions to the flora of extra-tropical South America. Lilloa **10**: 328.
59. *Apocynaceae and Asclepiadaceae. In* STANDLEY, P. C. and J. A. STEYERMARK. Studies of Central American Plants. IV. Field Mus. Publ. Bot. **23**: 78-81.
60. Miscellaneous new *Asclepiadaceae* from tropical America. Ann. Missouri Bot. Gard. **31**: 235-237.
61. Notes on some North American asclepiads. Ann. Missouri Bot. Gard. **31**: 363-370, *pl. 17.*

1945

62. Notes on some North American asclepiads. Ann. Missouri Bot. Gard. **32**: 369-371.

1946

63. About gloxinias. Missouri Bot. Gard. Bull. **34**: 247-256.
64. Amsonias. Missouri Bot. Gard. Bull. **34**: 158-160.
65. *Apocynaceae* and *Asclepiadaceae. In* MOLDENKE, H. N. Contributions to the flora of extra-tropical South America. Lilloa **11**: 193-195.
66. Memorabilia Filicum Panamensium. Am. Fern. J. **36**: 82-89.

1947

67. *Asclepiadaceae* (with E. E. CHEESMAN). *In* WILLIAMS, R. O., and E. E. CHEESMAN. Flora of Trinidad and Tobago. **2**: 162-175.
68. It's fun growing gloxinias, says writer in botanical magazine. Southern Florist and Nurseryman **59**: 9-10, 50. Jan. 17; and 11-12, 48. Jan. 24.
69. *Neobracea Howardii. In* HOWARD, R. A. Notes on some plants from Cuba. J. Arnold Arb. **28**: 125.
70. Notes on the "historical factor" in plant geography. Contr. Gray Herb. **165**: 12-25.
71. Review of "Plants and Plant Sciences in Latin America," ed. by FRANS VERDOORN. Am. Nat. **80**: 653-657.
72. Some dynamics of leaf variation in *Asclepias tuberosa.* Ann. Missouri Bot. Gard. **34**: 353-432.

1948

73. *Apocynaceae* and *Asclepiadaceae*. *In* Maguire, B., *et al.* Plant explorations in Guiana in 1944, chiefly to the Tafelberg and the Kaieteur Plateau-V. Bull. Torrey Bot. Club **75**: 553-561.
74. *Gynandropsis, Cleome,* and *Podandrogyne*. Ann. Missouri Bot. Gard. **35**: 139-147.
75. Miscellaneous new *Apocynaceae* and *Asclepiadaceae*. Ann. Missouri Bot. Gard. **35**: 233-238.

1949

76. New *Apocynaceae* of South America (with D. de Azumbuja). Ann. Missouri Bot. Gard. **36**: 543-548.

1950

77. *Liliaceae, Velloziaceae, Violaceae, Caricaceae, Loganiaceae, Apocynaceae,* and *Asclepiadaceae*. *In* Miscellanea taxonomica. I. Ann. Missouri Bot. Gard. **37**: 397, 398, 403-408.
78. The vegetation of the Great Rift Valley. (Review of W. Robyns' "Flore des Spermatophytes du Parc National Albert") Ecology **31**: 663, 664.

1951

79. Jesse More Greenman. (*1867-†1951). Ann. Missouri Bot. Gard **38**: 95-100, *portr.*
80. Studies in the *Apocynaceae*. VIII. An interim revision of the genus *Aspidosperma* Mart. & Zucc. Ann. Missouri Bot. Gard. **38**: 119-206, *pl. 1.*

1953

81. *Apocynaceae* and *Matelea*. *In* Steyermark, J. A., *et al.* Botanical Exploration in Venezuela III. Fieldiana **28**: 499-505, 510, 511.
82. Biometric evidence of natural selection in *Asclepias tuberosa*. Proc. Nat. Acad. **39**: 74-79.

1954

83. A correction in *Asclepias*. Ann. Missouri Bot. Gard. **41**: 261.
84. The North American species of *Asclepias* L. Ann. Missouri Bot. Gard. **41**: 1-211.
85. Why I like taxonomy—seven meditations. Bull. Torrey Bot. Club **81**: 87-90; reprinted in Missouri Bot. Gard. Bull. **42**: 91-96.

1956

86. A new Cuban *Matelea*. Contr. Ocas. Mus. Hist. Nat. Col. "De La Salle" **15**: 23, 24.

1957

87. *Rauwolfia*: Botany, Pharmacognosy, Chemistry & Pharmacology (with H. W. Youngken, E. Schlittler, & J. A. Schneider). pp. 149. Little, Brown, & Co., Boston.

1958

88. *Apocynaceae*. *In* Schultes, R. E. Plantae Austro-Americanae X. Americae Australis plantae novae vel ala ratione significantes. Bot. Mus. Leafl. **18**: 168-180.

1960

89. *Loganiaceae, Apocynaceae,* and *Asclepiadaceae*. *In* Miscellanea taxonomica. II. Ann. Missouri Bot. Gard. **47**: 73-80.
90. *Woytkowskia spermatochorda* Woodson, género y especie nuevas (*Tabernaemontanoideae*). Biota **3**: 89-91. [Authorized translation from Ann. Missouri Bot. Gard. **47**: 74-76. 1960.]

1962

91. Butterflyweed revisited. Evolution **16**: 168-185.

1963

92. My Debt to Paul C. Standley. *In* Williams, L. O. (ed). Homage to Standley. pp. 33-35. Chicago.

1964

93. *Apocynaceae*. *In* Steyermark, J. A. Notes on Ecuador plants. Phytologia **9**: 347, 348.
94. The geography of flower color in butterfly weed (annotations by S. Wright). Evolution **18**: 143-163, *pl. 1.*

Finding List

This list is arranged alphabetically according to the major fields of Woodson's interests. The arabic numerals following each category refer to the numbered papers of the preceding bibliography. Duplicate entries have been made where it was believed useful or necessary. I have included the dates of additional publications, in the Flora of Panama series, only when necessary to complete the listings in the section on monographic studies.

I. Anatomy: 25, 34, 42.
II. Biography: 79, 92.
III. Economic and Medicinal Botany: 1, 2, 7, 12, 57, 87.
IV. Horticulture: 17, 63, 64, 68.
V. Monographic Studies.
  a. *Apocynaceae:* 4, 5, 6, 7, 8, 9, 10, 13, 15, 16, 18, 19, 20, 21, 22, 24, 26, 27, 28, 30, 31, 33, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 49, 50, 51, 52, 57, 58, 59, 64, 65, 69, 73, 75, 76, 77, 80, 81, 87, 88, 89, 90, 93; see also Flora of Panama series of 1938 through 1942.
  b. *Asclepiadaceae:* 11, 21, 23, 25, 26, 44, 47, 52, 53, 54, 59, 60, 61, 62, 65, 67, 72, 75, 77, 81, 82, 83, 84, 86, 89, 91, 94; see also Flora of Panama series of 1937 through 1942.
  c. *Commelinaceae:* 29, 32, 55; see also Flora of Panama series of 1942 and 1944.
VI. Philosophy: 70, 85.
VII. Reviews: 71, 78.
VIII. Texts: 38, 87.
IX. Unclassified Miscellaneous: 3, 14, 48, 66, 74, 77, 89.

INDEX TO THE "CONTRIBUTIONS TOWARD A FLORA OF PANAMA" AND TO THE "FLORA OF PANAMA" THROUGH MARCH 1965

COMPILED BY ANDRÉ ROBYNS[1, 2]

Missouri Botanical Garden and Department of Botany, Washington University, St. Louis, Missouri

From 1937 to 1943, under the direction of Dr. Robert E. Woodson, Jr., seven *Contributions toward a Flora of Panama* were published in the ANNALS OF THE MISSOURI BOTANICAL GARDEN. The purpose of these *Contributions* was to "embody records of vascular plants previously described but hitherto not known to occur in Panama and the descriptions of novelties to science contributed, as far as possible, by specialists of the various plant families" (Ann. Missouri Bot. Gard. **24:** 176. 1937).

In 1943, the first fascicle of Part **2** of the *Flora of Panama* was published with Dr. Robert E. Woodson, Jr. as principal editor. The *Flora,* which is a compilation of the indigenous and naturalized vascular plants of the Republic of Panama, following generally the system of Engler & Prantl, is also published in the ANNALS OF THE MISSOURI BOTANICAL GARDEN. Up to the time of Dr. Woodson's death, and, since 1956, with the support of the National Science Foundation, Washington, D.C., 20 fascicles had been published:

Part **2,** complete with 3 fascicles
Part **3,** complete with 5 fascicles
Part **4,** complete with 5 fascicles
Part **5,** with 3 fascicles (incomplete)
Part **7,** complete with 4 fascicles (lacking title page and index)

Each of the above Parts of the *Flora* has two paginations: the first by virtue of its being a part of the ANNALS, the second a superimposed continuous pagination. *References to the* Flora *should always be to the former,* i.e. to volume number and pagination of the ANNALS.

The second pagination noted above rested upon the fact that all material of each Part was published in systematic order. It is no longer feasible to obtain manuscripts in such systematic order, and two changes in editorial policy have accordingly been made:

1) Dual pagination has been discontinued. Part **5,** however, will be concluded in the earlier manner.

2) Families expected to occur in the *Flora* have been assigned numbers from 1 to 184 as stated in Ann. Missouri Bot. Gard. **51:** iii-iv. 1964.

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[1]Supported by National Science Foundation Grant GB-170.

[2] I wish to thank Dr. G. B. Van Schaack for his constructive suggestions concerning this index.

ANN. MISSOURI BOT. GARD. **52**(3): 234-247. 1965.

Families (or suitable parts thereof) will be published with their assigned numbers as manuscripts are available. Those wishing to do so can eventually gather these into Parts, since each 'family publication' will be so printed as to begin on a right-hand page.

Since Dr. Woodson's death Part **5**, fascicle 4 and Part **6**, families 92, 104, 114, 116 and 117 have been published with the continued support of the National Science Foundation.

So far some 67 botanists, both American and European, have contributed in one way or another to the *Contributions* or to the *Flora* itself: Allen Caroline K., Allen P. H., Amshoff G. J. H., Bailey L. H., Barnhart J. H., Blake S. F., Burger W. C., Camp W. H., Clausen R. T., Constance L., Croizat L., Cuatrecasas J., Cutak L., Dandy J. E., Dewolf G. D., Jr., Dodson C. H., Duke J. A., Dwyer J. D., Epling C. C., Exell A. W., Fries R. E., Gleason H. A., Gregory D. P., Greenman J. M., Hermann F. J., Howard R. A., Jonker F. P., Kidd H. J., Killip E. P., Leonard E. C., Lundell C. L., Manning W. E., Mathias Mildred E., Maxon W. R., McClintock Elizabeth, McVaugh R., Moldenke H. N., Morton C. V., Muller C. H., Munz P. A., Nevling L. I., Jr., O'Neill F. H., Pennell F. W., Perry L. M., Pfeifer H. W., Raeder Katherine, Rhodes D. G., Rizzini C. T., Robyns A., Rollins R. C., Schery R. W., Schubert Bernice G., Schweinfurth C., Seibert R. J., Smith A. C., Smith C. E., Jr., Smith L. B., Standley P. C., Steyermark J. A., Svenson H. K., Swallen J. R., Trelease W., Van Royen P., Williams L. O., Wimmer F. E., Woodson R. E., Jr. & Yunker T. G.

A. *Contributions toward a Flora of Panama.*

Based upon Collections by Expeditions from the Missouri Botanical Garden Tropical Station, Balboa, C. Z.[3]

By Robert E. Woodson, Jr. & Russell J. Seibert (later Robert W. Schery[4]). Introduction.

Ann. Missouri Bot. Gard. **24:** 175-176, *pl. 5.* April 30. 1937.

I. Collections in the Provinces of Chiriquí, Coclé, and Panamá, by R. J. Seibert during the Summer of 1935.

Ann. Missouri Bot. Gard. **24:** 177-210, *pls. 6-8, fig. 1.* April 30, 1937.

Families (*Genera in italics*)	Authors	Pagination	Illustrations
Polypodiaceae	W. R. Maxon	180	
Cyperaceae	F. H. O'Neill	180	
Palmae	L. H. Bailey	180	
Bromeliaceae	L. B. Smith	180-181	
Amaryllidaceae	R. E. Woodson, Jr. & P. H. Allen	181	

[3]This subtitle is in general accurate only for the earlier *Contributions.*

[4]These *Contributions* were edited by Robert E. Woodson, Jr., assisted in Nos. 1-3 by Russell J. Seibert, and in Nos. 4-7 by Robert W. Schery.

Families (*Genera in italics*)	Authors	Pagination	Illustrations
Cannaceae	[5]	182	
Orchidaceae	C. Schweinfurth	182-185	
Piperaceae	W. Trelease	185-187	
Fagaceae		187	
Loranthaceae	W. Trelease	187-188	
Balanophoraceae		188	
Caryophyllaceae		188	
Ranunculaceae		188	
Lauraceae	R. E. Woodson, Jr.	188-189	
Cunoniaceae		189	
Rosaceae	L. H. Bailey	189	
Oxalidaceae	R. E. Woodson, Jr.	190	
Polygalaceae	S. F. Blake	190-191	
Vitaceae	R. E. Woodson, Jr. & R. J. Seibert	191-192	
Guttiferae		192	
Passifloraceae	E. P. Killip	192	
Thymelaeaceae	P. C. Standley	192-193	
Melastomaceae [i. e. Melastomataceae]	P. C. Standley	193-194	
Onagraceae	R. E. Woodson, Jr. & R. J. Seibert	194-196	
Araliaceae	P. C. Standley	196-197	
Ericaceae		197-198	
Myrsinaceae	P. C. Standley	198	
Asclepiadaceae	R. E. Woodson, Jr.	199-201	
Convolvulaceae	R. E. Woodson, Jr. & R. J. Seibert	201-202	
Orobanchaceae		202	
Gesneriaceae	C. V. Morton	202-205	
Acanthaceae	E. C. Leonard	205-208	Fig. 1
Rubiaceae	P. C. Standley	208-209	
Lobeliaceae	F. E. Wimmer	209-210	
Compositae	S. F. Blake	210	

II. Miscellaneous Collections during 1936-1938.
Ann. Missouri Bot. Gard. **25:** 823-840, *figs. 1-2.* November 28, 1938.

Polypodiaceae	W. R. Maxon	824	
Amaryllidaceae	R. E. Woodson, Jr.	824-825	
Burmanniaceae	F. P. Jonker	825	
Orchidaceae	C. Schweinfurth	825	
Piperaceae	W. Trelease	825-827	
Podostemonaceae	R. E. Woodson, Jr.	827-828	
Nyctaginaceae	P. C. Standley	828	
Magnoliaceae	R. J. Seibert	828-829	
Theaceae	P. C. Standley	829-830	
Passifloraceae	E. P. Killip	830	
Begoniaceae	P. C. Standley	830-831	
Combretaceae	P. C. Standley	831	

[5] Where no author is indicated, the treatments are presumed to be written by those responsible for the editing, as stated in footnote 4.

Families (*Genera in italics*)	Authors	Pagination	Illustrations
Myrsinaceae	P. C. Standley	832	
Apocynaceae		832-833	
Asclepiadaceae	R. E. Woodson, Jr.	833-835	Fig. 1
Orobanchaceae	R. E. Woodson, Jr.	835-836	Fig. 2
Rubiaceae	P. C. Standley	836-840	

III. Collections during the Summer of 1938, chiefly by R. E. Woodson, Jr., P. H. Allen, & R. J. Seibert.

Ann. Missouri Bot. Gard. **26:** 265-324, *pls. 18-23, figs. 1-3.* November 30, 1939.[6]

Lycopodiaceae	W. R. Maxon	272	
Isoetaceae	W. R. Maxon & C. V. Morton	272-273	
Hymenophyllaceae	W. R. Maxon	273	
Polypodiaceae	W. R. Maxon	273-274	
Ophioglossaceae	R. T. Clausen	274	
Cyperaceae	H. K. Svenson	274-275	
Bromeliaceae	L. B. Smith	275	Pl. 20
Juncaceae	R. E. Woodson, Jr.	275-276	
Musaceae	R. E. Woodson, Jr.	276-277	
Zingiberaceae	R. E. Woodson, Jr.	277-278	
Marantaceae	R. E. Woodson, Jr.	278-279	
Orchidaceae	L. O. Williams	279-287	Pl. 21
Rosaceae	R. E. Woodson, Jr.	287-288	
Alchemilla	L. M. Perry	287	
Polygalaceae	S. F. Blake	288	
Euphorbiaceae	P. C. Standley	289-290	
Dilleniaceae	P. C. Standley	290	
Tiliaceae		290-291	
Buxaceae	C. L. Lundell	291	
Celastraceae	C. L. Lundell	291-292	Pl. 22
Myrsinaceae	C. L. Lundell	292-294	
Vitaceae		294	
Guttiferae	P. C. Standley	294-295	
Myrtaceae	P. C. Standley	295	
Melastomaceae [i. e. Melastomataceae]	H. A. Gleason	295-296	
Lecythidaceae		296-297	
Vacciniaceae	W. H. Camp	297-298	
Gentianaceae	F. P. Jonker	298-299	
Halenia	C. K. Allen	298-299	
Apocynaceae	R. E. Woodson, Jr.	299-301	
Asclepiadaceae	R. E. Woodson, Jr.	301-305	Figs. 1-2
Cuscutaceae	T. G. Yunker	305-307	Fig. 3
Bignoniaceae		307-308	
Gesneriaceae	C. V. Morton	308-313	
Rubiaceae	P. C. Standley	313	
Caprifoliaceae		314	
Cucurbitaceae		314	
Compositae	S. F. Blake	314-317	Pl. 23
Senecio	J. M. Greenman	314	

[6] Misprinted as November 30, 1929.

IV. Miscellaneous Collections, chiefly by Paul H. Allen.
Ann. Missouri Bot. Gard. **27:** 265-364, *pls. 31-36, figs. 1-2.* September 25, 1940.

Families (*Genera in italics*)	Authors	Pagination	Illustrations
Marsileaceae	W. R. Maxon	265	
Polypodiaceae	W. R. Maxon	265-266	
Gramineae	J. R. Swallen	266-267	
Araceae	P. C. Standley	267	
Eriocaulaceae	H. N. Moldenke	268-269	
Bromeliaceae	L. B. Smith	269-270	
Liliaceae	R. E. Woodson, Jr.	270-271	
Dioscoreaceae	C. V. Morton	271	
Zingiberaceae		271	
Orchidaceae	L. O. Williams	271-286	Pls. 31-36
Piperaceae	W. Trelease	287-307	
Loranthaceae	R. E. Woodson, Jr. & R. W. Schery	307-310	
Phoradendron	W. Trelease	307-309	
Menispermaceae	P. C. Standley	310-311	
Cruciferae		311	
Capparidaceae	P. C. Standley	311-312	
Rosaceae		312	
Oxalidaceae	R. E. Woodson, Jr.	312-313	
Rutaceae	C. L. Lundell	313-314	
Euphorbiaceae	P. C. Standley	314-315	
Sapindaceae	P. C. Standley	315-317	
Rhamnaceae	C. V. Morton	318	
Tiliaceae	P. C. Standley	318	
Malvaceae	P. C. Standley	319	
Marcgraviaceae	R. E. Woodson, Jr., partim R. W. Schery, partim	319-321	
Guttiferae	P. C. Standley	321	
Loasaceae		321	
Begoniaceae	P. C. Standley	321-323	
Cactaceae	L. Cutak	323	
Myrtaceae	P. C. Standley	323-324	
Onagraceae	P. A. Munz	324	
Araliaceae	A. C. Smith, partim P. C. Standley & A. C. Smith, partim	324-327	
Ericaceae	W. H. Camp, partim A. C. Smith, partim	327-329	
Theophrastaceae	C. L. Lundell	329-330	
Loganiaceae	C. V. Morton	330	
Gentianaceae	F. P. Jonker	330-331	
Apocynaceae	R. E. Woodson, Jr.	331-333	
Asclepiadaceae	R. E. Woodson, Jr.	333-334	Fig. 1
Convolvulaceae	P. C. Standley	334-335	
Hydrophyllaceae		335	
Verbenaceae	H. N. Moldenke	335-336	
Solanaceae	P. C. Standley, partim C. V. Morton, partim	336-337	
Labiatae	C. C. Epling	337-338	
Scrophulariaceae	F. W. Pennell	338-341	
Gesneriaceae	C. V. Morton	341	
Lentibulariaceae	J. H. Barnhart	341	

Families (*Genera in italics*)	Authors	Pagination	Illustrations
Rubiaceae	P. C. Standley	341-346	
Valerianaceae	P. C. Standley	346-347	
Campanulaceae (Lobelioideae)	R. McVaugh	347-353	Fig. 2

V. Collections chiefly by Paul H. Allen, & by Robert E. Woodson, Jr. & Robert W. Schery.

Ann. Missouri Bot. Gard. **28:** 409-491, *pls. 19-25, figs. 1-2.* November 27, 1941.

Lycopodiaceae	W. R. Maxon	409	
Polypodiaceae	W. R. Maxon	409	
Taxaceae	P. C. Standley	409-411	
Eriocaulaceae	H. N. Moldenke	411	
Bromeliaceae	L. B. Smith	411-414	Pl. 19
Liliaceae		414	
Amaryllidaceae		414-415	
Dioscoreaceae	C. V. Morton	415	
Marantaceae		415	
Orchidaceae	L. O. Williams	415-425	Pls. 20-25
Piperaceae	W. Trelease	426	
Loranthaceae	R. E. Woodson, Jr.	426-427	
Balanophoraceae		427	
Annonaceae	R. W. Schery	427-429	
Cunoniaceae	R. E. Woodson, Jr.	429	
Connaraceae	J. A. Steyermark	430	
Oxalidaceae	R. E. Woodson, Jr. & R. W. Schery	431	
Rutaceae	C. L. Lundell	431-432	
Polygalaceae	S. F. Blake	432-433	
Celastraceae	C. L. Lundell	433	
Vitaceae		433	
Loasaceae		433	
Begoniaceae	L. B. Smith & B. G. Schubert	434	
Melastomaceae [i. e. Melastomataceae]	H. A. Gleason	434-437	
Araliaceae	A. C. Smith	437-438	
Vacciniaceae	A. C. Smith	438-452	
Theophrastaceae	C. L. Lundell	452-453	
Myrsinaceae	C. L. Lundell	453-459	
Gentianaceae	C. K. Allen, partim J. A. Steyermark, partim	459-461	
Apocynaceae	R. E. Woodson, Jr.	461-462	
Asclepiadaceae	R. E. Woodson, Jr.	462-463	
Convolvulaceae	R. W. Schery	463-464	
Verbenaceae	H. N. Moldenke	464	
Labiatae	C. C. Epling	464	
Solanaceae	C. V. Morton	464-465	
Gesneriaceae	C. V. Morton	465	
Acanthaceae	E. C. Leonard	465-469	Figs. 1-2
Cucurbitaceae		469	
Rubiaceae	P. C. Standley	469-472	
Compositae	S. F. Blake	472-476	

VI. Collections chiefly by H. von Wedel in Bocas del Toro.
Ann. Missouri Bot. Gard. **29:** 317-379, *pls. 30-34, 1 fig.* December 18, 1942.

Families *(Genera in italics)*	Authors	Pagination	Illustrations
Gramineae	J. R. Swallen	317-322	Fig.
Cyclanthaceae	R. E. Woodson, Jr.	322-324	
Commelinaceae		324	
Liliaceae	R. E. Woodson, Jr.	325-326	
Smilacaceae	C. V. Morton	326	
Dioscoreaceae	C. V. Morton	327	
Iridaceae		327	
Musaceae		327-329	
Zingiberaceae	R. E. Woodson, Jr.	329-331	
Cannaceae		331	
Marantaceae	R. E. Woodson, Jr.	331-335	
Burmanniaceae		336	
Orchidaceae	L. O. Williams	336-350	Pls. 30-34
Chloranthaceae		350	
Lacistemaceae		350	
Moraceae	P. C. Standley	350-351	
Capparidaceae	R. W. Schery	351-352	
Leguminosae		352	
Meliaceae		352	
Malpighiaceae		352	
Dichapetalaceae	R. E. Woodson, Jr.	353	
Euphorbiaceae	L. Croizat	353-357	
Hippocrateaceae		357-358	
Icacinaceae	R. A. Howard	358	
Sapindaceae		358	
Quiinaceae	P. C. Standley	358-359	
Tiliaceae	P. C. Standley	359	
Bombacaceae	R. E. Woodson, Jr.	359-360	
Sterculiaceae	R. W. Schery	360-361	
Dilleniaceae	C. V. Morton	361	
Ochnaceae		361	
Marcgraviaceae		361	
Guttiferae	R. W. Schery	362	
Violaceae	C. V. Morton	362-363	
Flacourtiaceae		363	
Turneraceae	C. V. Morton	363	
Caricaceae		363	
Cactaceae	L. Cutak	363	
Thymeliaceae [i. e. Thymelaeaceae]		364	
Onagraceae		364	
Loganiaceae		364	
Apocynaceae	R. E. Woodson, Jr.	364-365	
Asclepiadaceae	R. E. Woodson, Jr.	365-366	
Boraginaceae	R. W. Schery	366	
Solanaceae		366	
Bignoniaceae	R. W. Schery	367-368	
Lentibulariaceae	C. V. Morton	368	
Rubiaceae	P. C. Standley	368	
Cucurbitaceae		369	

VII. Miscellaneous Collections, chiefly by H. von Wedel, in Bocas del Toro. Ann. Missouri Bot. Gard. **30:** 83-96, *figs. 1-2.* March 22, 1943.

Families *(Genera in italics)*	Authors	Pagination	Illustrations
Bromeliaceae	L. B. Smith	83-85	Fig. 1
Moraceae	P. C. Standley	85	
Nyctaginaceae	P. C. Standley	85-86	
Annonaceae	R. W. Schery	86-87	
Saxifragaceae		88	
Leguminosae	R. W. Schery	88-93	Fig. 2
Malpighiaceae	R. W. Schery	93-95	
Icacinaceae		95	
Begoniaceae	L. B. Smith & B. G. Schubert	95	
Myrtaceae	R. W. Schery	95-96	
Rubiaceae	P. C. Standley	96	

B. *Flora of Panama.*

By Robert E. Woodson, Jr. & Robert W. Schery[7] & Collaborators.

Family Numbers	Families (*Genera in italics*)	Authors	ANNALS Volume	ANNALS Pagination	FLORA OF PANAMA Part	FLORA OF PANAMA Pagination	Illustrations	Date of Publication
1	Cycadaceae	R. E. Woodson, Jr.	**30**(2)	97-98	**2**(1)	1-2	Fig. 1	June 15, 1943
2	Taxaceae	R. E. Woodson, Jr.	**30**(2)	98-99	**2**(1)	2-3		June 15, 1943
3	Typhaceae	R. E. Woodson, Jr.	**30**(2)	99	**2**(1)	3	Fig. 2	June 15, 1943
3a	Potamogetonaceae	R. E. Woodson, Jr.	**30**(2)	99	**2**(1)	3		June 15, 1943
4	Alismaceae	R. E. Woodson, Jr.	**30**(2)	100-103	**2**(1)	4-7	Fig. 3	June 15, 1943
5	Butomaceae	R. E. Woodson, Jr.	**30**(2)	103-104	**2**(1)	7-8	Fig. 4	June 15, 1943
6	Triuridaceae	R. E. Woodson, Jr.	**30**(2)	104	**2**(1)	8	Fig. 5	June 15, 1943
7	Gramineae	J. R. Swallen	**30**(2)	104-280	**2**(1)	8-184	Figs. 6-31	June 15, 1943
8	Cyperaceae	H. K. Svenson	**30**(3)	281-325	**2**(2)	185-229	Figs. 32-43, Pl.1	Sept 30, 1943
9	Palmaceae [i.e. Palmae]	L. H. Bailey	**30**(3)	327-396	**2**(2)	231-300	Figs. 44-69	Sept 30, 1943
10	Cyclanthaceae	R. E. Woodson, Jr.	**30**(3)	396-403	**2**(2)	300-307	Figs. 70-72	Sept 30, 1943
11	Araceae	P. C. Standley	**31**(1)	1-60	**2**(3)	405-464[8]	Figs. 73-92	March 31, 1944
12	Lemnaceae	R. E. Woodson, Jr.	**31**(1)	60-62	**2**(3)	464-466		March 31, 1944
13	Mayacaceae	R. E. Woodson, Jr.	**31**(1)	62-63	**2**(3)	466-467	Fig. 93	March 31, 1944
14	Xyridaceae	R. E. Woodson, Jr.	**31**(1)	63-64	**2**(3)	467-468	Fig. 94	March 31, 1944
15	Eriocaulaceae	H. N. Moldenke	**31**(1)	65-71	**2**(3)	469-475	Fig. 95	March 31, 1944
16	Rapateaceae	R. E. Woodson, Jr.	**31**(1)	71-72	**2**(3)	475-476	Fig. 96	March 31, 1944
17	Bromeliaceae	L. B. Smith	**31**(1)	73-137	**2**(3)	477-541	Figs. 97-161	March 31, 1944
18	Commelinaceae	R. E. Woodson, Jr.	**31**(1)	138-151	**2**(3)	542-555	Figs. 162-166	March 31, 1944
19	Pontederiaceae	R. W. Schery	**31**(1)	151-157	**2**(3)	555-561	Figs. 167-171	March 31, 1944
	INDEX		**31**(1)	159-172	**2**	563-576		March 31, 1944
20	Juncaceae	R. E. Woodson, Jr.	**32**(1)	1-2	**3**(1)	1-2	Fig. 1	Feb 28, 1945
21	Liliaceae	R. E. Woodson, Jr.	**32**(1)	2-6	**3**(1)	2-6	Figs. 2-4	Feb 28, 1945
22	Smilacaceae	C. V. Morton	**32**(1)	6-11	**3**(1)	6-11	Figs. 5-6	Feb 28, 1945
23	Haemodoraceae	R. E. Woodson, Jr.	**32**(1)	11-12	**3**(1)	11-12	Fig. 7	Feb 28, 1945
24	Amaryllidaceae	R. E. Woodson, Jr.[9]	**32**(1)	12-25	**3**(1)	12-25	Figs. 8-17	Feb 28, 1945
	Bomarea	E. P. Killip	**32**(1)	14-17	**3**(1)	14-17	Figs. 9-10	Feb 28, 1945
25	Velloziaceae	R. E. Woodson, Jr.	**32**(1)	25-26	**3**(1)	25-26		Feb 28, 1945
26	Dioscoreaceae	C. V. Morton	**32**(1)	26-33	**3**(1)	26-33	Figs. 18-20	Feb 28, 1945
27	Iridaceae	R. E. Woodson, Jr.	**32**(1)	34-42	**3**(1)	34-42	Figs. 21-24	Feb 28, 1945
28	Burmanniaceae	F. P. Jonker	**32**(1)	42-47	**3**(1)	42-47	Figs. 25-27	Feb 28, 1945

[7] Dr. Robert W. Schery acted as junior editor until end of 1952.
[8] Because of a printing error, the pagination of Part **2**(3) was incorrectly started with p. 405. There are no pages numbered 309-404.
[9] The author of the genus *Zephyranthes* is R. W. Schery, according to a written communication of R. W. Schery.

Family Numbers	Families (*Genera in italics*)	Authors	ANNALS Volume	ANNALS Pagination	FLORA OF PANAMA Part	FLORA OF PANAMA Pagination	Illustrations	Date of Publication
29	Musaceae	R. E. Woodson, Jr.	**32**(1)	48-57	**3**(1)	48-57	Figs. 28-34	Feb 28, 1945
30	Zingiberaceae	R. E. Woodson, Jr.	**32**(1)	57-73	**3**(1)	57-73	Figs. 35-41	Feb 28, 1945
31	Cannaceae	R. E. Woodson, Jr.	**32**(1)	74-80	**3**(1)	74-80	Figs. 42-44	Feb 28, 1945
32	Marantaceae	R. E. Woodson, Jr.	**32**(1)	81-105	**3**(1)	81-105	Figs. 45-63	Feb 28, 1945
33	Orchidaceae, 1	L. O. Williams	**33**(1)	1-140	**3**(2)	107-246	Figs. 64-119	March 8, 1946
	Orchidaceae, 2	L. O. Williams	**33**(4)	315-404	**3**(3)	247-336	Figs. 120-147	Dec 7, 1946
	Orchidaceae, 3	P. H. Allen	**36**(1)	1-132	**3**(4)	337-468	Figs. 148-185	March 21, 1949
	Orchidaceae, 4	P. H. Allen	**36**(2)	133-245	**3**(5)	469-581	Figs. 186-213	June 18, 1949
	INDEX		**36**(2)	247-257	**3**	583-593		June 18, 1949
34	Piperaceae	T. G. Yuncker	**37**(1)	1-120	**4**(1)	1-120	Figs. 1-23	March 31, 1950
35	Chloranthaceae	L. I. Nevling, Jr.	**47**(2)	81-83	**4**(2)	121-123	Fig. 24	Aug 5, 1960
36	Lacistemaceae	L. I. Nevling, Jr.	**47**(2)	84-87	**4**(2)	124-127	Figs. 25-26	Aug 5, 1960
37	Salicaceae	R. E. Woodson, Jr.	**47**(2)	87	**4**(2)	127		Aug 5, 1960
38	Myricaceae	L. I. Nevling, Jr.	**47**(2)	88-89	**4**(2)	128-129	Fig. 27	Aug 5, 1960
39	Juglandaceae	W. E. Manning	**47**(2)	90-92	**4**(2)	130-132	Fig. 28	Aug 5, 1960
40	Corylaceae	L. I. Nevling, Jr.	**47**(2)	93-94	**4**(2)	133-134	Fig. 29	Aug 5, 1960
41	Fagaceae	C. H. Muller	**47**(2)	95-104	**4**(2)	135-144	Fig. 30	Aug 5, 1960
42	Ulmaceae	L. I. Nevling, Jr.	**47**(2)	105-113	**4**(2)	145-153	Figs. 31-35	Aug 5, 1960
43	Moraceae	R. E. Woodson, Jr.	**47**(2)	114-178	**4**(2)	154-218	Figs. 36-62	Aug 5, 1960
	Sorocea	W. C. Burger	**47**(2)	121-122	**4**(2)	161-162	Fig. 38	Aug 5, 1960
	Ficus	G. D. DeWolf, Jr.	**47**(2)	146-165	**4**(2)	186-205	Figs. 54-57	Aug 5, 1960
44	Urticaceae	E. P. Killip	**47**(2)	179-198	**4**(2)	219-238	Figs. 63-69	Aug 5, 1960
45	Proteaceae	L. I. Nevling, Jr.	**47**(2)	199-203	**4**(2)	239-243	Figs. 70-71	Aug 5, 1960
46	Loranthaceae	C. T. Rizzini	**47**(4)	263-290	**4**(3)	245-272	Figs. 72-82	Feb 7, 1961
47	Opiliaceae	L. I. Nevling, Jr.	**47**(4)	291-292	**4**(3)	273-274	Fig. 83	Feb 7, 1961
48	Olacaceae	L. I. Nevling, Jr.	**47**(4)	293-302	**4**(3)	275-284	Figs. 84-86	Feb 7, 1961
49	Balanophoraceae	L. I. Nevling, Jr.	**47**(4)	303-308	**4**(3)	285-290	Figs. 87-89	Feb 7, 1961
50	Aristolochiaceae	H. W. Pfeifer[10]	**47**(4)	309-323	**4**(3)	291-305	Figs. 90-102	Feb 7, 1961
51	Polygonaceae	J. A. Duke	**47**(4)	323-359	**4**(3)	305-341	Figs. 103-109	Feb 7, 1961
	Coccoloba	R. A. Howard	**47**(4)	340-353	**4**(3)	322-335	Figs. 107-108	Feb 7, 1961
52	Chenopodiaceae	J. A. Duke	**48**(1)	1-6	**4**(4)	343-348	Fig. 110	April 3, 1961
53	Amaranthaceae	J. A. Duke	**48**(1)	6-50	**4**(4)	348-392	Figs. 111-121	April 3, 1961

[10] Dr. Pfeifer's name was misspelled: Pfeiffer, in the publication.

Family Numbers	Families (*Genera in italics*)	Authors	ANNALS Volume	ANNALS Pagination	FLORA OF PANAMA Part	FLORA OF PANAMA Pagination	Illustrations	Date of Publication
54	Nyctaginaceae	R. E. Woodson, Jr.[11]	**48**(1)	51-65	**4**(4)	393-407	Figs. 122-126	April 3, 1961
55	Batidaceae	R. E. Woodson, Jr.	**48**(1)	66	**4**(4)	408		April 3, 1961
56	Phytolaccaceae	Katherine Raeder	**48**(1)	66-79	**4**(4)	408-421	Figs. 127-131	April 3, 1961
57	Aizoaceae	L. I. Nevling, Jr.	**48**(1)	80-85	**4**(4)	422-427	Figs. 132-134	April 3, 1961
58	Portulacaceae	L. I. Nevling, Jr.	**48**(1)	85-89	**4**(4)	427-431	Figs. 135-136	April 3, 1961
59	Caryophyllaceae	J. A. Duke	**48**(1)	90-106	**4**(4)	432-448	Figs. 137-141	April 3, 1961
60	Nymphaeaceae	J. A. Duke	**49**(3-4)	137-143	**4**(5)	449-455	Figs. 142-143	May 27, 1963
61	Ceratophyllaceae	J. A. Duke	**49**(3-4)	144	**4**(5)	456		May 27, 1963
62	Ranunculaceae	J. A. Duke	**49**(3-4)	144-153	**4**(5)	456-465	Figs. 144-146	May 27, 1963
63	Berberidaceae	J. A. Duke	**49**(3-4)	154-156	**4**(5)	466-468	Fig. 147	May 27, 1963
64	Menispermaceae	D. G. Rhodes	**49**(3-4)	157-172	**4**(5)	469-484	Figs. 148-151	May 27, 1963
65	Magnoliaceae	J. E. Dandy	**49**(3-4)	173-176	**4**(5)	485-488	Fig. 152	May 27, 1963
66	Winteraceae	J. E. Dandy	**49**(3-4)	177-178	**4**(5)	489-490	Fig. 153	May 27, 1963
67	Annonaceae	R. E. Fries	**49**(3-4)	179-213	**4**(5)	491-525	Figs. 154-166	May 27, 1963
68	Myristicaceae	J. A. Duke	**49**(3-4)	214-225	**4**(5)	526-537	Figs. 167-170	May 27, 1963
69	Monimiaceae	J. A. Duke	**49**(3-4)	225-239	**4**(5)	537-551	Figs. 171-174	May 27, 1963
	INDEX		**49**(3-4)	240-255	**4**	552-567		May 27, 1963
70	Lauraceae	Caroline K. Allen	**35**(1)	1-68	**5**(1)	1-68	Figs. 1-42	March 22, 1948
71	Hernandiaceae	R. E. Woodson, Jr.	**35**(1)	68-71	**5**(1)	68-71	Fig. 43	March 22, 1948
72	Papaveraceae	R. E. Woodson, Jr.	**35**(1)	71-75	**5**(1)	71-75	Fig. 44	March 22, 1948
72a	Tovariaceae	R. E. Woodson, Jr.	**35**(1)	75	**5**(1)	75		March 22, 1948
76	Moringaceae	R. E. Woodson, Jr.	**35**(1)	75	**5**(1)	75		March 22, 1948
73	Capparidaceae	R. E. Woodson, Jr.	**35**(1)	75-99	**5**(1)	75-99	Figs. 45-51	March 22, 1948
74	Cruciferae	R. C. Rollins	**35**(1)	99-106	**5**(1)	99-106	Figs. 52-53	March 22, 1948
75	Resedaceae	R. E. Woodson, Jr.	**37**(2)	121	**5**(2)	107		June 2, 1950
76	Moringaceae[12]	R. E. Woodson, Jr.	**37**(2)	121	**5**(2)	107		June 2, 1950
77	Crassulaceae	R. E. Woodson, Jr.	**37**(2)	121-124	**5**(2)	107-110		June 2, 1950
78	Podostemonaceae	P. Van Royen	**37**(2)	124-137	**5**(2)	110-123	Figs. 54-61	June 2, 1950
79	Saxifragaceae	Elizabeth McClintock	**37**(2)	137-145	**5**(2)	123-131	Figs. 62-63	June 2, 1950
80	Cunoniaceae	R. E. Woodson, Jr.	**37**(2)	145-147	**5**(2)	131-133	Fig. 64	June 2, 1950
81	Rosaceae	R. McVaugh	**37**(2)	147-178	**5**(2)	133-164	Figs. 65-73	June 2, 1950
	Rubus	L. H. Bailey	**37**(2)	154-159	**5**(2)	140-145	Figs. 66-67	June 2, 1950

[11] With the collaboration of H. J. Kidd.

[12] Elaboration of Note on p. 75.

Family Numbers	Families (*Genera in italics*)	Authors	ANNALS Volume	ANNALS Pagination	FLORA OF PANAMA Part	FLORA OF PANAMA Pagination	Illustrations	Date of Publication
82	Connaraceae	R. E. Woodson, Jr.	**37**(2)	178-183	**5**(2)	164-169	Fig. 74	June 2, 1950
83	Leguminosae	R. W. Schery	**37**(2)	184-185	**5**(2)	170-171		June 2, 1950
	Legum.-Mimosoideae	R. W. Schery	**37**(2)	185-314	**5**(2)	171-300	Figs. 75-104	June 2, 1950
	Legum.-Caesalpinoideae	R. W. Schery[13]	**38**(1)	1-94	**5**(3)	301-394	Figs. 105-132	March 22, 1951
	Legum.-Papilionoideae partim	J. D. Dwyer	**52**(1)	1-54	**5**(4)	395-448	Figs. 133-145	March 31, 1965
	Lonchocarpus	F. J. Hermann[14]	**52**(1)	39-47	**5**(4)	433-441	Fig. 142	March 31, 1965
92	Meliaceae	C. E. Smith, Jr.	**52**(1)	55-79	**6**	[15]	Figs. 1-6	March 31, 1965
104	Hippocrateaceae	C. H. Dodson & A. Robyns	**52**(1)	81-98	**6**		Fig. 1	March 31, 1965
114	Tiliaceae	A. Robyns	**51**(1-4)	1-35	**6**		Figs. 1-9	Nov 30, 1964
116	Bombacaceae	A. Robyns	**51**(1-4)	37-68	**6**		Figs. 1-9	Nov 30, 1964
117	Sterculiaceae	A. Robyns	**51**(1-4)	69-107	**6**		Figs. 1-7	Nov 30, 1964
	Theobroma	J. Cuatrecasas	**51**(1-4)	89-97	**6**			Nov 30, 1964
130	Passifloraceae	R. E. Woodson, Jr.	**45**(1)	1-22	**7**(1)	1-22	Figs. 1-2	March 20, 1958
131	Caricaceae	R. E. Woodson, Jr.	**45**(1)	22-31	**7**(1)	22-31	Figs. 3-6	March 20, 1958
132	Loasaceae	R. E. Woodson, Jr.	**45**(1)	32-40	**7**(1)	32-40	Figs. 7-10	March 20, 1958
133	Begoniaceae	L. B. Smith & B. G. Schubert	**45**(1)	41-67	**7**(1)	41-67	Figs. 11-20	March 20, 1958
134	Cactaceae	R. E. Woodson, Jr.[16]	**45**(1)	68-91	**7**(1)	68-91	Figs. 21-28	March 20, 1958
135	Thymelaeaceae	R. E. Woodson, Jr.	**45**(2)	93-97	**7**(2)	93-97	Figs. 29-30	May 27, 1958
136	Lythraceae	L. I. Nevling, Jr.	**45**(2)	97-115	**7**(2)	97-115	Figs. 31-35	May 27, 1958
137	Lecythidaceae	R. E. Woodson, Jr.	**45**(2)	115-136	**7**(2)	115-136	Figs. 36-42	May 27, 1958
138	Rhizophoraceae	D. P. Gregory	**45**(2)	136-142	**7**(2)	136-142	Figs. 43-44	May 27, 1958
139	Combretaceae	A. W. Exell	**45**(2)	143-164	**7**(2)	143-164	Figs. 45-51	May 27, 1958
140	Myrtaceae	G. J. H. Amshoff	**45**(2)	165-201	**7**(2)	165-201	Figs. 52-62	May 27, 1958
141	Melastomataceae	H. A. Gleason	**45**(3)	203-304	**7**(3)	203-304	Figs. 63-93	Oct 28, 1958
142	Onagraceae	P. A. Munz	**46**(3)	195-221	**7**(4)	305-331	Figs. 94-98	Oct 15, 1959
143	Haloragidaceae	R. E. Woodson, Jr.	**46**(3)	221-223	**7**(4)	331-333	Fig. 99	Oct 15, 1959
144	Araliaceae	L. I. Nevling, Jr.	**46**(3)	223-242	**7**(4)	333-352	Figs. 100-104	Oct 15, 1959
145	Umbelliferae	M. E. Mathias & L. Constance	**46**(3)	242-254	**7**(4)	352-364	Figs. 105-107	Oct 15, 1959
146	Cornaceae	R. E. Woodson, Jr.	**46**(3)	254-256	**7**(4)	364-366	Fig. 108	Oct 15, 1959

[13] The genera *Cynometra* and *Copaifera* were reviewed by J. D. Dwyer.

[14] Misprinted as F. I. Hermann.

[15] See introduction, p. 234.

[16] One species, *Epiphyllum gigas*, is described by R. E. Woodson, Jr. & L. Cutak.

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GRADUATE STUDENTS OF ROBERT E. WOODSON, JR.

COMPILED BY WALTER H. LEWIS

Missouri Botanical Garden and Department of Botany,
Washington University, St. Louis, Missouri

Below are listed the students who obtained graduate degrees under the direction of Dr. Robert E. Woodson, Jr. while he was a member of the Department of Botany at Washington University. Two factors have made the compilation of this list difficult and probably incomplete. These are the absence of all University records regarding major professors prior to 1955 (detailed files were destroyed because of space limitations), and the necessity that Dr. Woodson, as a member of the University Graduate Council, sign as thesis chairman for several students who in fact completed their research under other professors who were not members of the Council. Consequently, the list has been compiled by examining theses acknowledgments (when given) and by discussions and correspondence with Drs. Anderson, Andrews, Cutler, Schery, Van Schaack and others whose help is much appreciated.

ANDREWS, HENRY N., JR.

A study of the secondary wood of certain mesozoic and tertiary conifers, M.A. 1937; On the stelar anatomy of the pteridosperms, with particular reference to the secondary wood, Ph.D. 1939.

Department of Botany, University of Connecticut, Storrs.

BURGER, WILLIAM C.

A revision of the genus *Sorocea* and allied genera of the New World, Ph.D. 1961.

Chicago Natural History Museum, Chicago, Illinois.

COOPER, ROBERT C.

The Australian and New Zealand species of *Pittosporum*, Ph.D. 1953.

Auckland Institute & Museum, Auckland, New Zealand.

FREYTAG, GEORGE F.

A monographic study of the genus *Guazuma*, M.A. 1950.

Escuela Agricola Panamericana, Tegucigalpa, Honduras.

GILLETT, JOHN M.

A revision of the North American species of *Gentianella* Moench., Ph.D. 1952.

Plant Research Institute, Central Experimental Farm, Department of Agriculture, Ottawa, Ontario, Canada.

GREGORY, DAVID P.

The *Rhizophoraceae* of Panama, M.A. 1957.

Department of Botany, University of Maine, Orono.

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HOLM, RICHARD W.

The American species of *Sarcostemma*, M.A. 1948; The genus *Sarcostemma*, Ph.D. 1950.

Department of Biological Sciences, Stanford University, Palo Alto, California.

HOU, DING

A revision of the genus *Celastrus*, Ph.D. 1955.

Rijksherbarium, Leiden, Netherlands.

HUNTER, GORDON E.

Revision of Mexican and Central American *Saurauia*, Ph.D. 1963.

Department of Biological Sciences, Murray State College, Murray, Kentucky.

ILTIS, HUGH H.

A revision of the New World species of *Cleome*, Ph.D. 1952.

Department of Botany, University of Wisconsin, Madison.

KALTENTHALER, HENRY J., III

A revision of the verticillate species of *Bouvardia*, M.A. 1956.

University City High School, St. Louis, Missouri.

LAY, KO KO

A revision of the genus *Heliocarpus*, M.A. 1949; The American species of *Triumfetta*, Ph.D. 1950.

11 West Moat Road, Mandalay, Burma.

LEÓN, JORGE

The Central American and West Indian species of *Inga*, Ph.D. 1953.

Instituto Inter-Americano de Ciencias, Lima, Peru.

MEYER, ELIANE (MRS. EDWARD NORMAN)

The genus *Vallesia*—a systematic study, M.A. 1955.

Department of Botany, Rutgers—The State University, New Brunswick, New Jersey.

MEYER, FREDERICK G.

Valeriana in North America and the West Indies, Ph.D. 1949.

U. S. National Arboretum, Washington, D. C.

MOHLENBROCK, ROBERT H., JR.

A revision of the genus *Stylosanthes*, Ph.D. 1957.

Department of Botany, Southern Illinois University, Carbondale.

MOORE, JOHN A.

The vascular anatomy of the flower in the papilionaceous *Leguminosae*, Ph.D. 1934.

Deceased, formerly Department of Botany, Louisiana Polytechnic Institute, Ruston.

NEVLING, LORIN I., JR.

The *Lythraceae* of Panama, M.A. 1957; A revision of the genus *Daphnopsis*, Ph.D. 1959.

Arnold Arboretum & Gray Herbarium, Harvard University, Cambridge, Massachusetts.

Ngan, Phung Trung

A preliminary survey of the genus *Wrightia,* M.A. 1962; A revision of the genus *Wrightia,* Ph.D. 1963.

Department of Botany, University of Saigon, Viet Nam.

Ownbey, Gerald B.

Monograph of the North American species of *Corydalis,* Ph.D. 1947.

Department of Botany, University of Minnesota, Minneapolis.

Pfeifer, Howard W.

The *Aristolochiaceae* of Panama, M.A. 1960; A revision of the hexandrous species of *Aristolochia* in greater North America, Ph.D. 1963.

Department of Botany, University of Connecticut, Storrs.

Raeder, Katherine (Mrs. Bruce Burns)

The *Phytoloccaceae* of Panama, M.A. 1958.

11634 Chenault Street, Los Angeles 49, California.

Rao, A. S.

A revision of *Rauvolfia* with particular reference to the American species, Ph.D. 1956.

Botanical Survey of India, Poona 1, India.

Rhodes, Donald G.

The *Menispermaceae* of Panama, M.A. 1958.

Department of Biology, Southeast Missouri State College, Cape Girardeau, Missouri.

Rogers, David J.

A revision of *Stillingia* in the New World, Ph.D. 1951.

Department of Botany, Colorado State University, Fort Collins.

Safwat, Fuad M.

Anatomy of the flower of *Cynanchum laeve* (Michx.) Pers., M.A. 1960; The floral morphology of *Secamone* and the evolution of the pollinating apparatus in *Asclepiadaceae,* Ph.D. 1962.

Department of Biology, University of Massachusetts at Boston.

Seibert, Russell J.

A study of *Hevea,* with its economic aspects in the Republic of Peru, Ph.D. 1947.

Longwood Gardens, Kennett Square, Pennsylvania.

A FRUCTIFICATION OF ANACHOROPTERIS FROM THE MIDDLE PENNSYLVANIAN OF ILLINOIS

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and University of Connecticut, Storrs

Abstract

An unattached massive compact fructification, apparently a fertile pinna, of *Anachoropteris* is described. The outstanding features of the fructification include a distinctly anachoropterid xylary strand in the central axis, the sporangial aggregation and compact pinnate arrangement, the multiseriate annulus of the sporangium with a pseudoapical plate, and spores congeneric with *Raistrickia*. Comparisons are made with the massive, fertile pinnae and sporangia of *Botryopteris globosa*.

Introduction

The genus *Anachoropteris* Corda, known since 1845 from histologically preserved non-laminate foliar members is a coenopterid fern that has become much better known in the past ten years. Stem anatomy of *A. clavata* Graham was first elucidated by Delevoryas and Morgan (1954a), and *Tubicaulis*-like similarities were pointed out; a striking feature, however, was the origin of shoots from foliar members in *A. clavata* (Delevoryas & Morgan, 1954a) as well as *A. involuta* (Hall, 1961). In a recent discovery of an apparent principle axis of *Anachoropteris*, Hall (1961) established the organic continuity of petioles of *A. involuta* Hoskins basally with a stem of *Tubicaulis* sp. which differed somewhat from *T. multiscalariformis* Delevoryas & Morgan and from *T. stewartii* Eggert.

An extensive bibliography of earlier studies of *Anachoropteris* has been assembled by Corsin (1937), and although there are numerous well known occurrences of foliar members (original basis for all known species) of *Anachoropteris*, natural relationships with other ferns have remained tenuous from lack of information pertaining to stems, laminate foliage and particularly fructifications.

The laminate foliage and fructification of *Anachoropteris* and certain *Tubicaulis* types of plants have not been reported previously, with the exception of *Chorionopteris gleichenioides*, a laminate synangiate-bearing pinnule which was doubtfully attributed to *Anachoropteris pulchra* Corda by Kubart (1916).

Materials and Techniques

The coal ball specimen, Illinois #6441, containing the sporangial aggregate was collected by us at the Sahara Coal Company mine, 4 miles northwest of Carrier Mills, Illinois, from the Illinois No. 6 (Herrin) coal, of the Carbondale formation which is Middle Pennsylvanian in age.

The coal ball was cut into three slabs to determine the total extent of the fructification which was about 30 mm in length. Three series of peel preparations were made from them. The lowermost part was slightly curved and permitted

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longitudinal sections of a portion of the central axis; the uppermost portion was somewhat crushed and provided material for spore and sporangial macerations.

Preservation of the fructification is somewhat irregular. The sporangial walls and spores are especially well preserved as is the central xylary axis and many smaller xylary divisions; however, the cortical or ground tissue of the axis and its ramifications are poorly preserved throughout and there is evidence of some crushing or compaction of the aggregate prior to impregnation with calcium carbonate. Uncleared spores were obtained from the uppermost section by use of dilute HCl, and following the general procedure of Mamay (1957) small selected fragments of the fructification were treated in 5% HCl. Sporangia were cleared in a strong Schulze's solution.

All figured specimens are deposited in the paleobotanical collections of the University of Illinois, Urbana.

Description

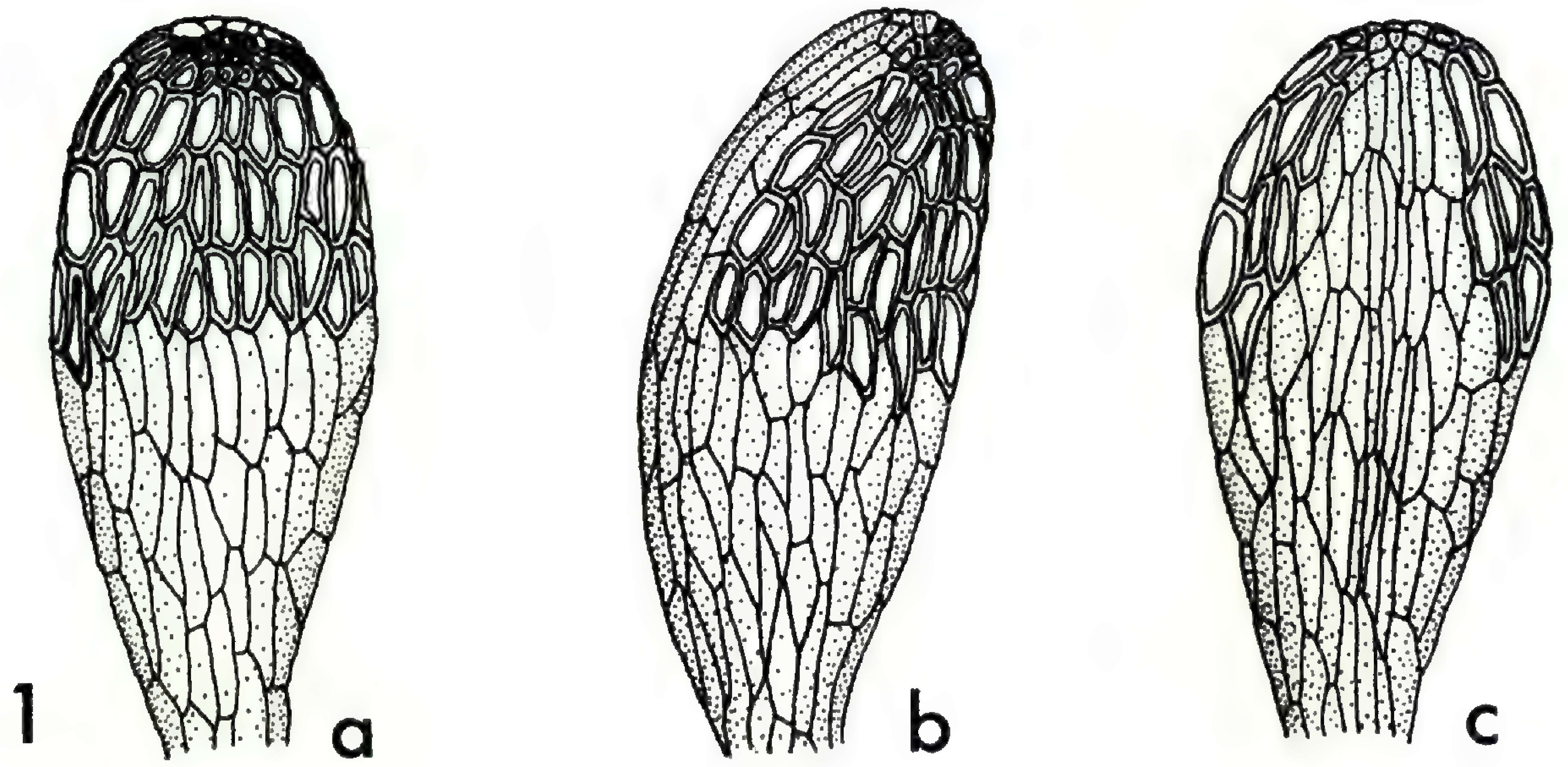
The fossil described here is a massive unit aggregation of sporangia with a ramifying axis that contains a characteristic *Anachoropteris* foliar vascular strand. There is a maximum of about 800 sporangia visible in a single section and we estimate the total number in the fructification to be approximately 30,000.

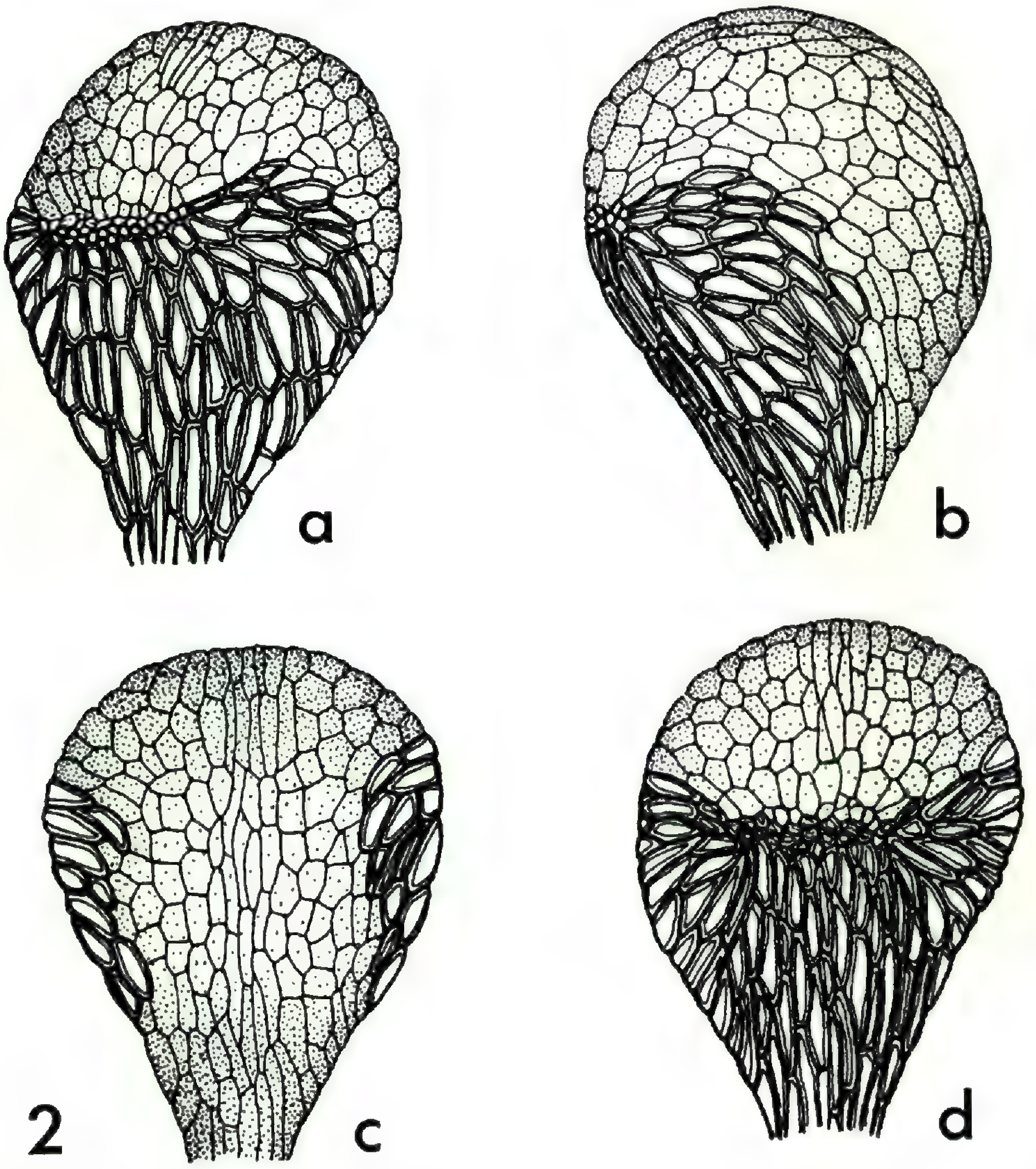
In its gross form the fossil resembles the sporangial aggregate of *Botryopteris globosa* Darrah and it is problematical as to whether it represents an entire frond or simply a fertile pinna. A part of the problem in using these terms lies in the difficulty of correlating precisely the morphological units of the coenopterids with those of modern ferns; this is considered in a little more detail in the Discussion section.

In an oblique transverse plane through which the fertile structure was sectioned it was possible to trace both upper and lowermost limits; in the lowermost exposed section it is somewhat elliptical, with dimensions of approximately 30 × 11 mm; a part of this is shown in Fig. 1. The main axis which contains an *Anachoropteris* foliar xylem strand (Fig. 1, 4) produced distichously arranged branches which divided to form the ultimate divisions that bore the sporangia. The contained spores are of the *Raistrickia* type and have been noted previously in coal balls from the No. 6 (Herrin) coal; this is, however, the first time that it has been possible to correlate them with the genus *Anachoropteris*.

A representative section through the fructification is shown in Fig. 1 where three types of structures may be noted. The greater part of the fossil consists of several thousands of sporangia, there is a main axis with an anachoropterid vascular strand which is conspicuous in the upper portion of the photograph, and there are numerous pinna divisions which for the most part are poorly preserved.

The strand which is referred to as the main axis of the fructification enters the latter along the narrow axis in peel A124. It is about 1.5 mm in diameter and penetrates the sporangial aggregate for about 18 mm, then makes a right angle turn and continues through the greater part of the aggregate. The vascular strand is rather massive; the two ends are recurved and almost globose as seen in section





Text Figure 1. Sporangia of *Anachoropteris* sp.; annulus indicated by double-lined walls. *a.* face or annulus side of sporangium with pseudo-apical plate; *b.* lateral view of sporangium showing extent of annulus development on each side; *c.* view on opposite side from *a* showing well defined region of dehiscence and lateral occurrence of annulus. Specimen No. 6441C. 50×.

Text Figure 2. Sporangia of *Botryopteris globosa;* annulus indicated by double-lined walls. *a.* view of sporangium showing face and lateral extent of annulus; *b.* lateral view of sporangium; *c.* view on opposite side from *d* showing region of dehiscence and lateral occurrence of annulus; *d.* face or annulus view. Specimen No. 6017B, Herrin (No. 6) Coal. 50×.

(Fig. 4-7); they taper quickly to the sides which are slender, being for the most part two cells thick; the "upper" part of the strand, as it is oriented in Figs. 5-7, is again thicker and consists of two distinct ridges and a median trough.

Figures 5-7 reveal the manner in which primary branches depart. In Fig. 5 a bulge appears at the left which represents an early stage in the formation of the vascular supply to a primary branch; in Fig. 6 this has actually separated and in Fig. 7 a second branch trace is starting to depart in the same manner on the right side. Figures 8 and 9 show such primary branches some distance from the main axis. In the one shown in Fig. 9 a tertiary branch trace is departing from one side (the lower side as the photograph is oriented on the plate), following the pattern of branching in the main axis.

The sporangia and their contained spores are beautifully preserved and display some interesting and significant features. In addition to the photographs (Fig. 10-22), Text Fig. 1 shows various aspects of the wall structure; these restoration drawings are based on our studies of the sporangia as they appear in the peel preparations (sections) as well as the maceration preparations (Fig. 15-17, 19, 21). The latter were especially informative and leave no reasonable doubt as to the accuracy of the drawings.

The length of the sporangium is more than two times its maximum width which is attained slightly distal to the mid-region. It is thus pyriform and being also slightly curved it has the form of a banana somewhat swollen toward the distal end. Sporangia measured in near-median longitudinal sections ranged from 0.78 to 0.95 mm in length and they have an average diameter of 0.38 mm. In its general morphology the sporangium consists of the following: a distinct stalk that is somewhat attenuated and crushed in most cases; a wall that is one cell thick at maturity with a multiseriate annulus 4-6 cells high which composes one-third to one-half of the distal portion of the sporangium (Text Fig. 1a, 1b), and a clearly defined region of dehiscence with a maximum width of 4-5 cells.

Dehiscence was longitudinal and the narrow elongate cells in this region extend sub-apically from a small group of non-indurated cells down to near the base of the sporangium. On the opposite face of the sporangium the distalmost portion of the annulus consists of small indurated cells; these are not located at the extreme tip of the sporangium but, rather, are slightly to one side and may be referred to as an off-center or near-apical cluster. They merge with relatively thin-walled cells of similar size on the dehiscence face of the sporangium, as noted above. Extending downward and laterally to some extent the annulus cells are larger and elongate parallel with the axis of the sporangium. The annulus extends around each side of the distal portion and is quite sharply defined (Text Fig. 1c). The line of distinction between the annulus cells and those composing the lower (proximal) half of the sporangium is rather irregular and there is considerable variability in the number of cells in a vertical segment of the annulus.

The spores (Figs. 18, 20, 22) are referable to the genus *Raistrickia* but, to the best of our knowledge, they are not specifically comparable with any that have been described from North America. The spore body is spherical to roundly triangular and ranges in diameter from 35-55 μ, the mean diameter being 40 μ

in a sample of 50 spores from slides 1909-1911. The arms of the trilete mark (Fig. 20) vary from 10-18 μ in length with 13 μ being typical. The spores are conspicuously ornamented with large appendages or spines which are spaced about 6-8 μ apart and are present on both proximal and distal surfaces. The appendages attain lengths of 10-13 μ, they are 2-6 μ thick and are either divided into two blunt ends or have a knob-like termination; some are marked by transverse rings or bars (Fig. 22).

Discussion

It is interesting to discover in *Anachoropteris* a fructification in the form of a massive sporangial aggregate very much like that of *Botryopteris*. (Murdy & Andrews, 1957). It is also possible that such organs characterize *Biscalitheca* (Mamay, 1957) and *Eopteridangium* (Andrews & Agashe, 1962); both are known from large apparent unit aggregates of sporangia although little is known about the vegetative structures and the affinities of *Eopteridangium* are obscure.

It has been stated that the Coenopterid ferns are a specialized group and consequently of little aid in understanding the origins of modern ferns. This is very likely the case with some of them; the highly complex nature of the sporangium wall in *Biscalitheca* and in *Monoscalitheca* (Abbott, 1961) would seem to indicate that these are specialized types and the same may hold for the unique *Stauropteris burntislandica*. Eggert (1964) has recently presented a good summary of our knowledge of the coenopterids and it is therefore not necessary to review the group in detail here.

We suggest that not all of the fossils assigned to the *Coenopteridales* are highly specialized and in particular *Botryopteris* and *Anachoropteris* may well be a point of origin for later fern groups. Considering first the sporangia, in both genera the annulus is a fairly large (in numbers) group of cells partially wrapped around the distal end. The cells are not strikingly different in size and form from the other cells, with the exception of those along the line of dehiscence; they are somewhat thicker walled, numerous and the annulus patch as a whole does not display a rigidly defined pattern. If we compare the sporangia here, with particular reference to the annulus, with those of ferns such as *Polypodium, Gleichenia* or *Anemia* the fossils seem much less specialized.

Of modern ferns that we are familiar with there does seem to be a strikingly close comparison with the sporangia of *Osmunda* (Hewitson, 1962). The sporangium of *Osmunda* is nearly spherical and thus more like that of *Botryopteris* than that of *Anachoropteris* in its general form. The annulus of Osmunda is a rather poorly defined patch of cells on one side, very much like that of the annulus in the two fossils if the number of cells was considerably reduced.

The distinctive compact aggregate form in which the sporangia are arranged in *Botryopteris* was at first regarded as unique and specialized. It is now evident that it was not unique and in either *Botryopteris* or *Anachoropteris* an expansion of the branch system could easily result in a structure like the fertile frond of *Osmunda cinnamomea*. When it is unfolding in the spring the fertile frond of O. *cinnamomea* is in fact a rather compact aggregation of sporangia not unlike the sporangial aggregates of the two fossil genera. The steles of *Botryopteris* and

Anachoropteris are of simple organization and could quite possibly be the Carboniferous predecessors of the Permian members of the *Osmundaceae.* We are aware of the distinctive nature of the foliar strands in *Botryopteris* and *Anachoropteris* which differ from the leaf traces of *Osmunda;* however, on points other than this the similarities greatly outweigh the differences and we suggest that these fossils represent a complex from which the *Osmundaceae* evolved.

Summary

A massive sporangial aggregate is described from the Carbondale formation, Middle Pennsylvanian, of Illinois. The sporangia are pyriform and slightly curved with an unspecialized group of annulus cells wrapped around the distal half with the exception of the dehiscence band; dehiscence was longitudinal. A conspicuous axis runs through the fructification which contains an anachoropterid vascular strand; this gives off two rows of primary branches which divide, probably several times, the ultimate branchlets bearing the sporangia in clusters. The spores are distinguished by numerous stout projections many of which have conspicuous cross-bands. It is suggested that *Botryopteris* and *Anachoropteris* are relatively unspecialized plants representing a group from which the *Osmundaceae* evolved.

Acknowledgement

This study was financed in large part by grants to one of us (HNA) from the National Science Foundation. We are also grateful to Mr. Lewis Gray of the University of Illinois for information that he has supplied us concerning *Raistrickia.*

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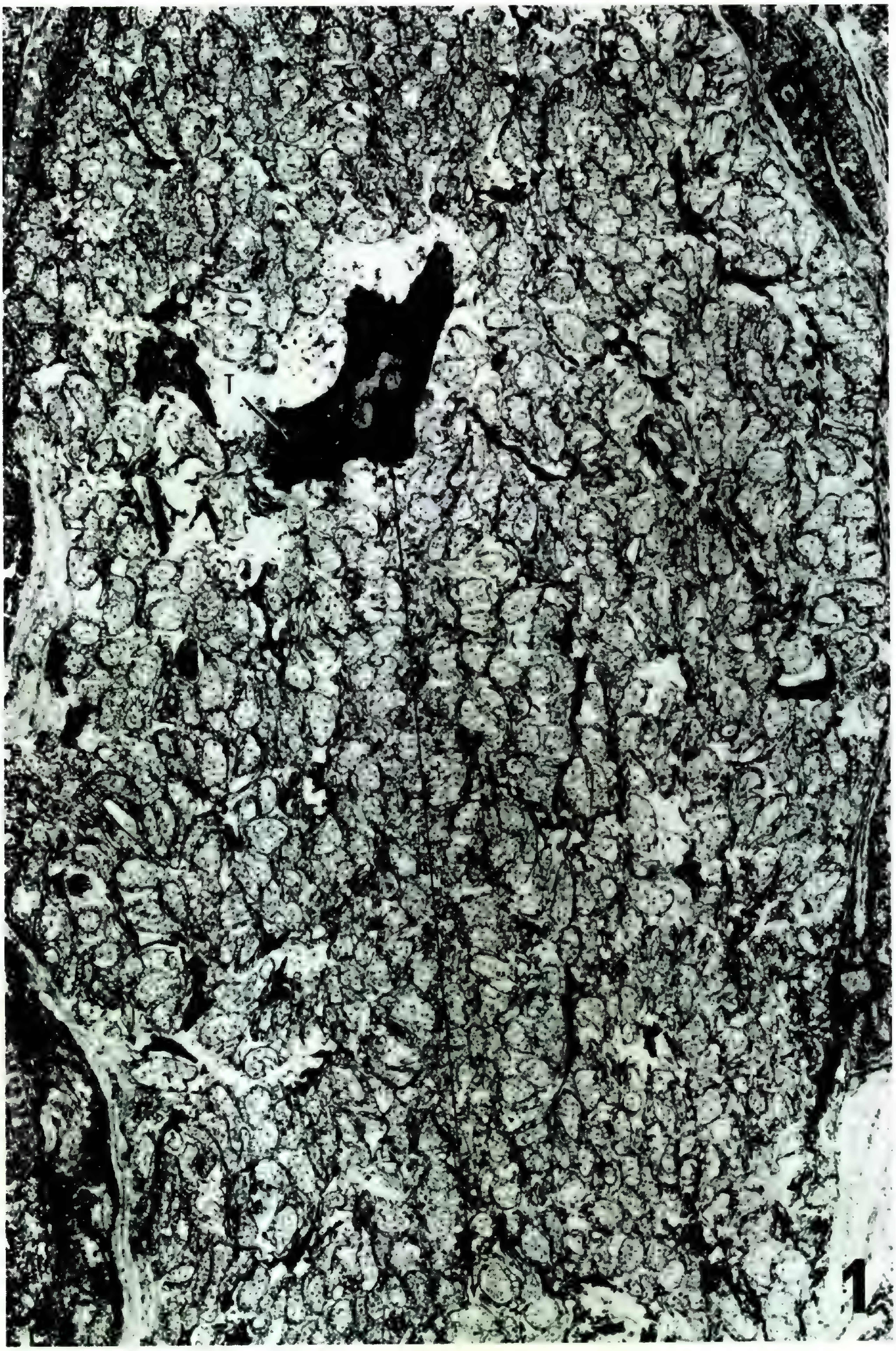

PLATE I. *Anachoropteris* sp.

Fig. 1. Oblique-transverse view of fructification with about two-thirds of the section of exposed sporangia. Central axis of pinnately branched fructification exhibits an involuted xylary strand surrounded by a blackened cortical zone. T, pinna trace from central axis. Black line indicates approximate separation zone of sporangia borne upon divisions from opposite sides of the fructification. AB-71/Slide 1896, 12×.

Plate II. *Anachoropteris* sp.

Fig. 2. Longitudinal section of one side of central axis near base of fructification with pinna trace departure, T. C, cavity in degraded black ground tissue: AB-111/Slide 1897, 35×. Fig. 3. Scalariform thickenings of tracheidal walls. AB-124/Slide 1898, 182×. Fig. 4. Trans-section of central axis of fructification with portions of attached pinnae, right and left. T, pinna trace; PG, pinna gap; P1, continuation of pinna from central axis; P2, secondary pinna order of division from central axis; IT, incipient pinna trace. AB-5/Slide 1899, 40×.

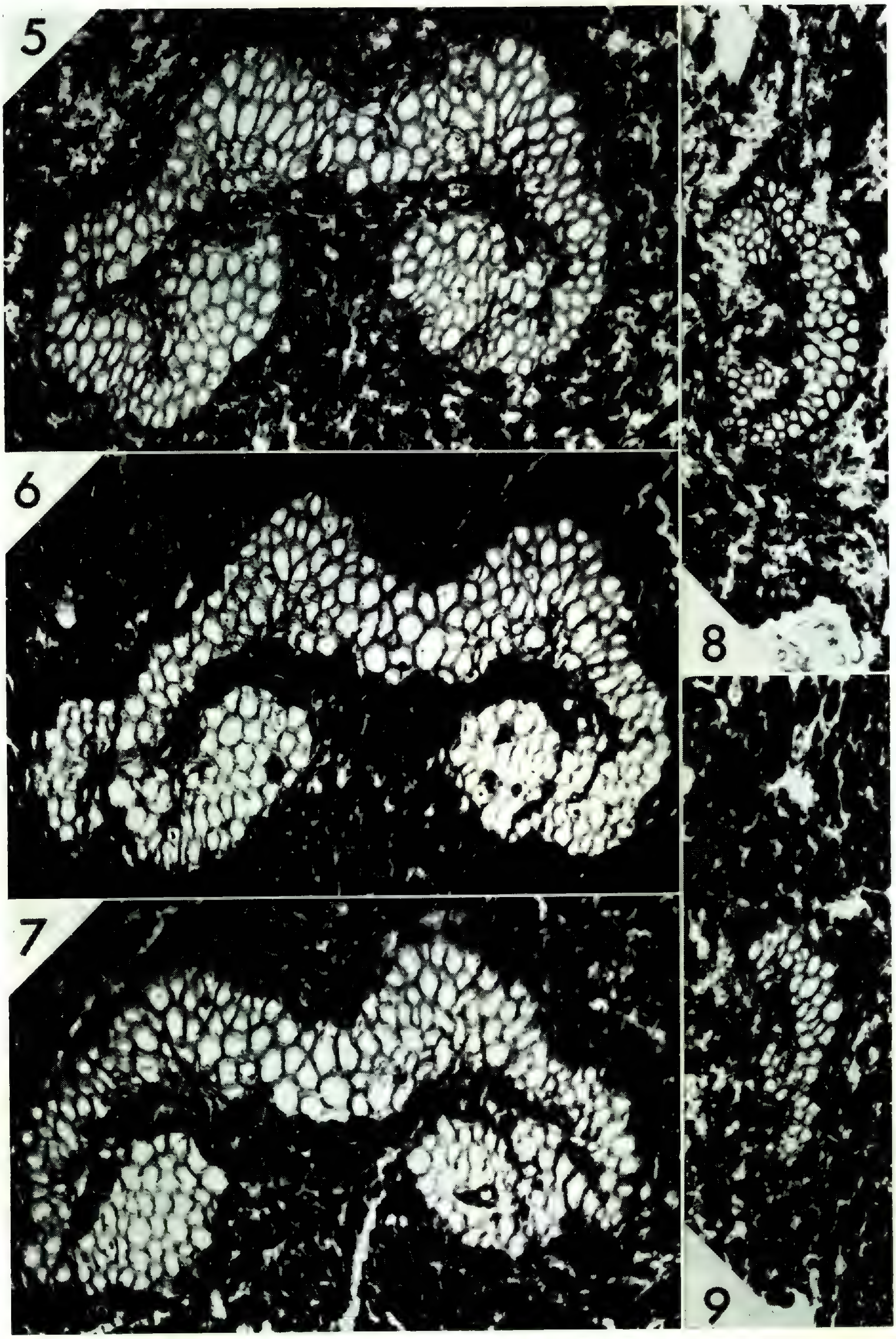

PLATE III. *Anachoropteris* sp.

Fig. 5-7. Representative sections from a serial sequence of transverse views of xylary strand of central axis of fructification. 124×. Fig. 5. Incipient pinna trace formation on left. AB-37/Slide 1900. Fig. 6. Incipient trace departure on left. AB-29/Slide 1901. Fig. 7. Incipient pinna trace formation on right. AB-19/Slide 1902. Fig. 8. Trans-section of first order of division of central axis with ground tissue in distal portion of fructification. CT-17/Slide 1903. 135×. Fig. 9. Trans-section of xylary strand of a secondary pinna division at a stage of incipient trace departure. AB-84/Slide 1904. 135×.

Plate IV. *Anachoropteris* sp.

Fig. 10 & 11. Longitudinal sections of sporangia showing attachments to ultimate foliar divisions. AB 9 Slide 1905 and BT 89/Slide 1906. 75×. Fig. 12. Trans-sections of sporangia; lower left with annulus oriented downward and region of dehiscence upward. BT 97/Slide 1907. 75×. Fig. 13. Longitudinal section with annulus cells on each side and part of indurated pseudo-apical plate terminally. BT 47/Slide 1908. 128×. Fig. 14. Trans-section of sporangium with slit of dehiscence on right. AB 71/Slide 1896. 128×.

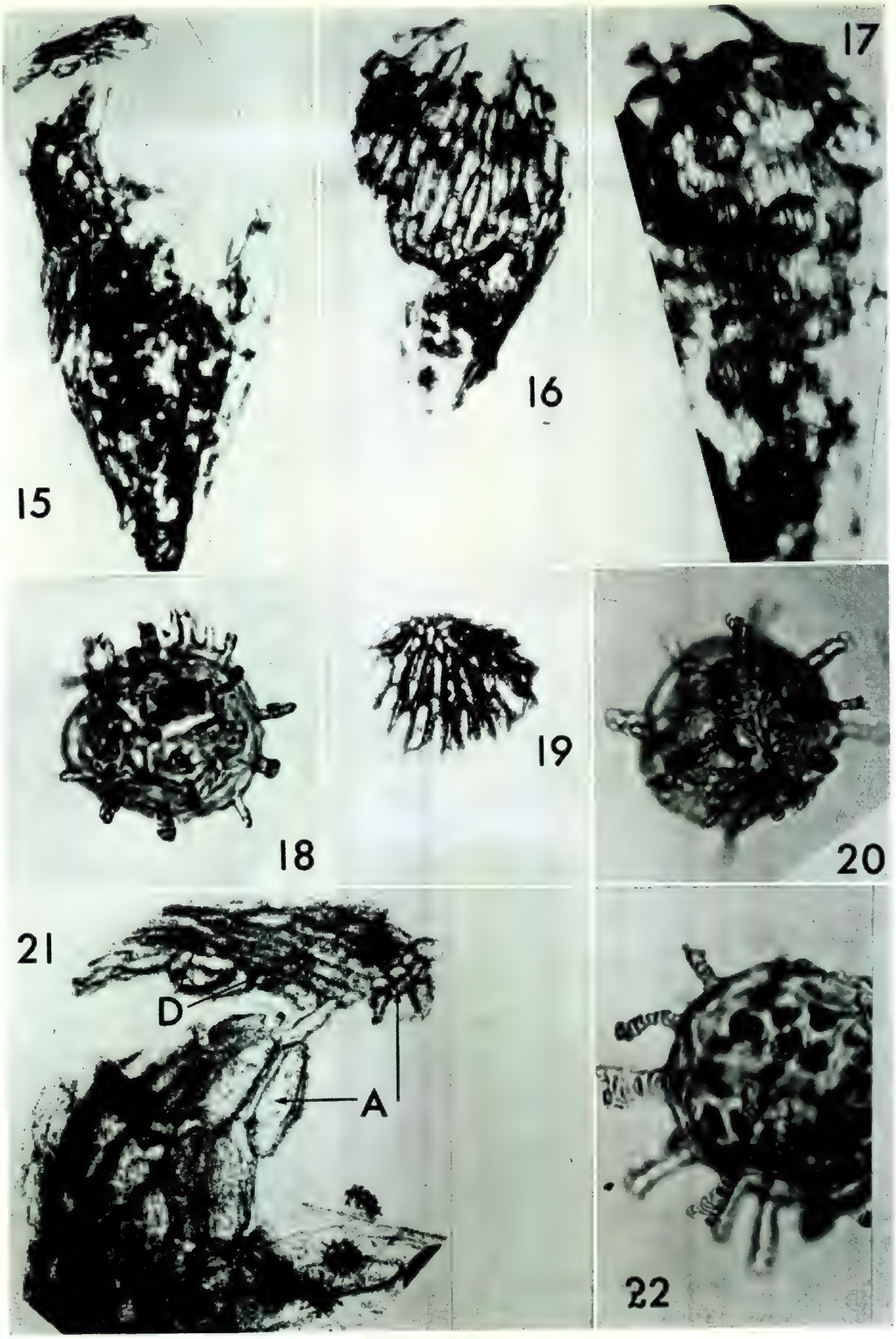

Plate V. *Anachoropteris* sp.

Fig. 15-22. Macerated sporangial fragments and spores. Fig. 15. Lateral view of sporangium with region of dehiscence to left and annulus face on right; large portion of annulus removed. Uppermost portion of sporangium shown enlarged in Fig. 21. Fig. 16. Fragment of face or annulus side of sporangium with cleared annulus cells occupying upper two thirds; small indurated cells of pseudo-apical plate absent. Fig. 17. Isolated intact sporangium as seen in annulus view while being cleared with Schulze's solution; see Text fig. 1a. Fig. 18. Spore of the *Raistrickia* type with spines in focus; note spine upon trilete suture. Diameters 38× 45μ. CT-5/Slide 1910. Fig. 19. Apical sporangial segment showing small indurated pseudo-apical place which terminates annulus. Fig. 20. Spore of the *Raistrickia* type in proximal view with triradiate mark in focus. Diameters 43 × 45μ. CT2/Slide 1909. Fig. 21. Partially cleared apical portion of sporangium shown in Fig. 15. A, small indurated cells apically terminating annulus and larger annulus cells which occupy lateral position; D, region of dehiscence. See Text Fig. 1b. Fig. 22. Enlarged view of barred spines of *Raistrickia* spores with several exhibiting division. CT-1/Slide 1911. 830×.

THE SOUTHERN CALIFORNIAN PRICKLY PEARS—INVASION, ADULTERATION, AND TRIAL-BY-FIRE[1]

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When Father Junipero Serra founded the Mission San Diego in 1769, he began unknowingly the transformation of the landscape of California and its vegetation. After founding of the missions, settlers from Mexico and Spain brought agriculture and livestock, including sheep. As range animals were taken from the Mediterranean region to Mexico and other parts of the world, weed seeds were carried along in the wool or hair and in mud on the hoofs. Wherever sheep walked or died weeds sprang up. Through many centuries of hybridizing and selection these plants were adapted to areas about dwellings of man and his cultivated fields and pasture lands. They had evolved in Mediterranean areas of summer drought disturbed by fire and over-grazing, and they were adjusted perfectly to the similar Californian climate and to the newly disturbed areas. Ultimately they reached an ecological dynamic equilibrium with the native species. This equilibrium shifts from year-to-year in correspondence with the highly erratic incidence of winter rainfall.

When the Franciscan Fathers established the series of missions through coastal southern California they brought with them, also, fruit-bearing plants from Mexico and Spain. These included grapes, figs, and other fruits of mild climates, among them the large cultivated fruit-tree cacti of Mexico—primarily of two kinds. These prickly pears have become known in the United States as the mission cacti, *Opuntia Ficus-Indica,* a spineless type, and *Opuntia megacantha,* a similar plant with flattened, white spines at each of the areoles (spine-bearing areas) on the joint (but with the spines of some joints tending to be brownish). These two plants are similar to each other, and the evolutionary origin of *Opuntia Ficus-Indica* from *Opuntia megacantha,* as the wild type, was postulated by David Griffiths (J. Hered. **5:** 222. 1914). Both are members of a complex of cultivated prickly pears abundant in Mexico, many of them representing horticultural forms or hybrids of *Opuntia Ficus-Indica.* The mission Fathers and others found these cacti not only useful for their fruit but important as a source of mucilaginous binding material for the adobe bricks of the mission buildings. In the course of time the two cacti were planted also on the great Spanish ranchos about both the ranch headquarters and the dwellings of ranch employees and other individuals, and they appeared wherever there were Spanish, Mexican, and, later, American settlers.

In many places the large cultivated prickly pears hybridize with the small native species as pointed out by Baxter (California Cactus 40. 1935). Recent field

[1] This paper is prepared with the financial assistance in studying the cacti of the United States and Canada of several grants-in-aid from the Claremont Graduate School, one from the Society of Sigma Xi for 1950, and three from the National Science Foundation, covering the periods from 1956 to 1959, 1959 to 1964, and 1965 to 1966. The aid in all phases of the work is acknowledged with gratitude.

studies, especially in Los Angeles, San Bernardino, Riverside, and Orange Counties, indicate this hybridization to be vastly more extensive than has been supposed. The introduced cacti often survive in the lowlands or on the edges of hills about the sites of old dwellings. Here and there they have spread a short distance, but they are restricted to the better-watered, deeper soils along washes in the valleys or at the mouths of canyons. However, their genes are given rapid air transportation by several species of native bees and by beetles, especially *Carpophilus pallipennis* (Say) (*Nitidulidae*). Sometimes the local hillside population of cacti includes plants with character combinations ranging from almost those of the mission cacti, usually of the spiny type known as *Opuntia megacantha,* to those of the native species, but more commonly the character combinations are restricted. In a few areas, the prevailing plants are near the end of the series approaching *Opuntia megacantha,* but this is rare. Commonly the population is composed of plants varying in characters from about those of the postulated F_1 generation to those of the native species, because individuals in this range of phenotypes are better-adapted to the dry, shallow soils of south-facing slopes where cacti are most abundant. The hillside populations away from the immediate coast are dominated mostly by plants of about the middle of this series, i.e., "quarter-breeds". On the other hand, gravelly or sandy places in the beds of dry washes, or shady areas beneath trees, or mountain areas are strongholds of varieties of the native species.

Fire has been a major factor in the evolution of prickly pears in southern California. Cacti do not grow in the chaparral or brushland because this is a fire type of vegetation burned over, on the average, once in five to thirty years. A hot chaparral fire cannot be survived by cactus plants. Even a summer grass fire sweeping through a patch of prickly pears is devastating, for small plants are killed outright and the larger ones often are killed, too, except sometimes for parts below ground or those sheltered, as by a piling up of cactus stem joints during the fire. From any living fragment new joints may arise. Among the weeds introduced into California from the Mediterranean region are many grasses, especially of the genus *Bromus,* and these have formed a dense cover in the lowlands and on hillsides. The modified grassy areas become like tinder in the dry summer months, and grass fires are intense and frequent. Thus, in each locality every few years for two centuries there has been a determination of which plants are best adapted to withstanding intense heat; the prickly pears have been subject to a rigid trial-by-fire.

Selection by fire has not favored the native species but the larger hybrid plants and especially those able to form dense patches from which grasses are more or less excluded. These thickets of cactus joints are vulnerable to fire only around the fringes. They form vigorous resistant centers which grow outward and occupy more and more space after each grass fire. The smaller native species, on the other hand, is enveloped in grass, and on the open hillsides each fire tends to reduce its numbers. For this reason, the tendency in the large areas of dry grass is toward the ascendency of a vast array of hybrid types about intemediate between the postulated F_1 generation and the small native species. Both morphological and chemical characters (Walkington, ined.) indicate this.

During the last half of the nineteenth century and almost two-thirds of the twentieth, all botanical authors have used the name *Opuntia occidentalis* for elements in the populations of hybrid cacti common everywhere except along the immediate coast. However, each author has had a different mental image of this species, for each has had in mind a different plant or range of plants in the vast hybrid swarm. Usually this has been one or a few of the many combinations about midway between the F_1 generation and the native species. No population can be reconciled with the description of *Opuntia occidentalis* appearing in any book or paper, for no two plants are alike and the total variation is extreme.[2] Thus, from the standpoint of classification, the common conception of "*Opuntia occidentalis*" is a will-o-the-wisp, for it was based in each book upon one or more transistory combinations of genes which would disappear with the individual plant(s) or the clone(s) upon which the description was based.

For several years the syntypes or original collections of *Opuntia occidentalis* Engelm. & Bigelow have been or loan from the Missouri Botanical Garden to Pomona College with the hope that the identity of the plants to which this name was applied could be established. The principal original collection was by Dr. J. M. Bigelow on the Whipple Expedition, which from 1852 to 1854 explored on horseback for a railroad route to the Pacific Ocean (that of the Santa Fe Railroad from Arkansas to Los Angeles), U. S. Senate Rept. Expl. & Surv. Route R. R. Pacific Ocean. Botany, **4:** *38, pl. 7, f. 1-2.* 1865. The place of collection was described on page 38, as follows: "On the western slope of the California mountains, from QuiqualGungo, east of Los Angeles, to San Pasquale and San Isabel [Santa Ysabel], northeast of San Diego, (A. Schott), at an elevation of 1,000 to 2,000 feet, in immense patches, often as large as half an acre." On page 16, it was described as follows: "At the Cajon Valley . . . At Cocomungo, in this valley, we [of the Whipple Expedition] found vast and dense patches of an Opuntia, nearly akin to O. *Engelmanni* . . . ." Quiqual Gungo and Cocomungo seem to be different transliterations of the Indian place name, which in modern usage must be Cucamonga. Most of the description of *Opuntia occidentalis* was drawn from the Cucamonga specimen, made up of a large joint and a fruit, though the habit of the plant and the flower characters were based upon a collection by Arthur Schott from San Pasquale in San Diego County, which includes in each of two herbarium specimens only a fragment of a joint and a flower (MO, US (photo), F 42740). The Schott collection, as shown especially by the specimen at the Chicago National History Museum, is of the small native species appearing in books as *Opuntia Vaseyi* or *Opuntia Covillei* or both. Because the main part of the description is drawn from the large joint and the fruit and seeds collected by Bigelow and because the illustrations were made from them, this collection must be designated as a lectotype (cf. below).

The identity of the Bigelow collection from Cucamonga, then, must determine which kind of plant was named *Opuntia occidentalis.* Study of cacti growing in the vicinity of Cucamonga is difficult because nearly the entire area has been

[2] This, of course, has worried the authors, for most of them have recognized the extreme complexity of the "species," even though the source of complexity was not understood.

plowed up for planting of vineyards or citrus trees. On the alluvial fans at the base of the San Gabriel Mountains the citrus groves are protected by *Eucalyptus* windbreaks, and in the shade of these trees the small native prickly pears flourish. Finally, on a water-spreading ground near the mouth of a canyon above Cucamonga one very large plant was found. This had joints nearly identical with but mostly larger than the one collected by Bigelow, but selection of a medium or small joint to be carried on horseback is understandable. The Cucamonga plant is the mission cactus, known as *Opuntia megacantha* Salm-Dyck. Consequently, the name combination *Opuntia occidentalis* cannot be used for any native Californian plant but only for the spiny mission cactus. Thus *Opuntia occidentalis* is merely a synonym for *Opuntia megacantha,* applied much earlier. Because *Opuntia megacantha* differs from the Indian fig only in presence of spines, it appears to be only one cultivar (horticultural variety) within one of the vast complexes of Mexican fruit trees for which the Linnaean name, *Opuntia Ficus-Indica,* may be all- or nearly all-inclusive. Thus *Opuntia occidentalis* and *Opuntia megacantha* are synonyms for *Opuntia Ficus-Indica* (L.) Miller.

With the name combination *Opuntia occidentalis* removed from the scene, the next question is, "What scientific name should be applied to the small inland native species and its varieties"? These plants are described in some books as *Opuntia Vaseyi,* and this name is applicable, even though the source of the type specimen, stated as Yuma, Arizona, is in error (cf. below) because of confusion of labels. *Opuntia Covillei* is valid and clear in its application; but it was published simultaneously with *Opuntia Vaseyi.* The name *Opuntia littoralis,* has been misused in nearly all the books for *Opuntia oricola* Philbrick, Cactus & Succ. J. **36:** 163, *3 figs.* 1964, a far different coastal plant. *Opuntia littoralis* Engelm. was based upon a specimen derived from a taxon related closely to *Opuntia Vaseyi,* as indicated below. In specific rank the epithet *littoralis,* properly applied, has priority in time of publication over all others, as indicated below in the formal treatment of the species.

The native juicy-fruited prickly pears of southern California include three major elements, as listed below. Probably each has been modified to some degree by introgression of genes from the mission cacti, especially from the spiny type.

1. *Opuntia littoralis* (Engelm.) Cockerell, composed of five varieties: *littoralis, Vaseyi, austrocalifornica, Piercei,* and *Martiniana,* described in this paper. *Spines acicular, not all yellow.*

2. *Opuntia phaeacantha* Engelm. vars. *major* and *discata*[3] (*Opuntia Engelmannii* of authors), both occurring on the desert side of the mountain axis and in

[3] Detailed discussion of the "*Opuntia Engelmannii*" problem is not included in this paper. As shown below, the epithet *Engelmannii* belongs to the spiny mission cactus. The proper name for the plant long known as *Opuntia Engelmannii* is *Opuntia phaeacantha* Engelm. var. **discata** (Griffiths) Benson & Walkington, comb. nov. (*Opuntia discata* Griffiths, Rept. Mo. Mot. Gard. **19:** 265, *pl. 27, upper.* 1908. *Opuntia Engelmannii* Salm-Dyck var. *discata* C. Z. Nelson, Galesburg [Illinois] Register, June 20, 1915, Trans. Ill. Acad. Sci. **12:** 124. 1919.) "The type is no. 7790 D. G[riffiths], collected in the foothills of the Santa Rita Mountains [Pima County], Arizona, April, 1905." Type: *Griffiths 7790,* US. Isotype: POM 287144 (on 2 sheets).

the eastern Mojave desert. In the works of Californian authors, these have been discussed in part under local names (e.g., *Opuntia mojavensis* and *Opuntia megacarpa*). *Spines* (at least some of them) *subulate, appearing flattened* (actually very narrowly elliptic in cross section), *not all yellow.*

3. *The coastal complex.* This includes the following elements characterized by only completely *yellow spines,* the spines of *Opuntia littoralis* and *Opuntia phaeacantha* being of other colors or only in part yellow or some spines yellow and the rest other colors. However, yellow spines of cacti turn black or dark gray in age or in specimens. *At least some spines in the areole are flattened.*

a. *Opuntia oricola* Philbrick, Cactus & Succ. J. **36:** 163, 3 *f.* 1964. This plant is distinctive, and it appears to be a natural taxon; however chemical tests (Walkington, ined.) indicate introgression from *Opuntia Ficus-Indica* (*megacantha*), and further study is necessary. *Opuntia chlorotica* Engelm. occurs in the deserts. *Opuntia oricola* resembles it in some ways, but a close relationship has not been established.

b. "Demissa," large plants with yellow spines. They are somewhat reminiscent of *Opuntia Lindheimeri* Engelm. of Texas and the adjacent Gulf Coast. Based upon *Opuntia demissa* Griffiths, Rept. Missouri Bot. Gard. **22:** 29, *pl.* 8. 1912.

Another type of prickly pear occurring along the coast perhaps includes *Opuntia semispinosa* Griffiths, Bull. Torrey Bot. Club **43:** 89. 1916. This plant, similar in some ways to *Opuntia littoralis,* will require further study. It shows possible affinity to *O. phaeacantha var. discata.*

Only *Opuntia littoralis* and its relationship to *Opuntia Ficus-Indica* are discussed fully in this paper.

1. Opuntia littoralis (Engelm.) Cockerell

Suberect or sprawling shrub usually 3-10 dm high and 6-12 dm in diam; trunk none; larger terminal joints green to somewhat or sometimes strongly glaucous, narrowly obovate or narrowly elliptic to broadly so or sometimes nearly orbiculate, 0.75 or 1.25-1.75 or 3 dm long, 0.5 or 0.75-1 or 1.25 dm broad, 1.2-2 cm thick; areoles 1.5-3 or 4.5 mm in diam, typically 1.5-2.8 cm apart; spines distributed over the entire joint or only the upper part (or in var. *austrocalifornica* none), brown, tan, pink, gray, or various combinations of these and yellow, 1-11 (or 0) per areole, spreading or some deflexed, usually straight, sometimes some curving, longer ones 2.5-5.6 or 6.9 cm long, basally up to 1 mm in diam, acicular, not barbed; glochids yellow, tan, or brown, 1.5-4.5 mm long; flower 5-7.5 cm in diam, 5-7.5 cm long; sepaloid perianth parts with the midribs green and the margins yellow or partly reddish or magenta, lanceolate to ovate-acuminate or to obdeltoid-cuneate or obovate, 6-31 mm long, 3-22 mm broad, acuminate to mucronate, nearly entire; petaloid perianth parts yellow with red or magenta bases or sometimes magenta or rose-purple, the largest ones obovate or obovate-cuneate, 2.5-5.5 cm long, 1.5-4 cm broad, rounded and mucronate, nearly entire; filaments yellow, 9-12 mm long; anthers yellow, 2.25 mm long; style yellowish, 1.2-1.9 cm long, 3-7 mm in greatest diam, swollen basally; stigmas 8-12, 3-4.5 mm long, rather thick; ovary in anthesis spineless or with a few small deciduous spines above; fruit reddish to reddish-purple, fleshy at maturity, with only small glochids, obovoid or narrowly so, about 3.5-4 (rarely 6) cm long, about 2.5-3.8 cm in diam, with the umbilicus cuplike, maturing after several months; seed light tan or gray, irregular but fundamentally nearly discoid, with the margin enclosing the embryo conspicuous and irregular, exceedingly variable in size, 3-6 mm in diam or length, 3-6 mm broad, 1.5 mm thick.

Table 1. Varieties of *Opuntia littoralis*.

	A. Var. *littoralis*	B. Var. *Vaseyi*	C. Var. *austrocalifornia*	D. Var. *Piercei*	E. Var. *Martiniana*
Glaucousness	Green, not glaucous	Moderate	Strong; joints bluish	Moderate	Moderate
Joint shape	Narrowly obovate or narrowly elliptic	Obovate or narrowly so	Narrowly obovate to nearly orbiculate	Narrowly obovate or elliptic to orbiculate	Obovate to orbiculate
Joint size	12.5-18.8 cm long, 7.5-10 or 11.8 cm broad	10-15 or 25 cm long, 7.5-10 or 15 cm broad	7.5-12.5 or 20 cm. long, 5-6.2 or 12 cm broad	12.5-20 or 30 cm long, 7.5-10 or 12.5 cm broad	12.5 or 17.5 cm long, 7.5-13.8 cm broad
Spine distribution	Over the entire joint	On nearly all of the joint	No spines or a few along the top of the joint	On nearly all of the joint	Usually on most or all of the joint
Spine color	Some gray, some yellow, some mixtures of these and red	Brown or dark gray	White, gray, straw color, or golden	Reddish with yellow or white tips	Red and yellow to gray
Spine length	3.1-4.7 cm	2.5-5.5 cm	0.6-1.2 or 2 cm	2.5 or 3.8-5 cm	2.5 or 3.8-6.9 cm
Spines per areole	5 to 11	1 to 4 or 6	0 or 1 to 2 and rudimentary	1 to 4 or 6	1 to 4 or 6
Flower color	Yellow	Yellow	Magenta	Yellow	Yellow or the center reddish
Geographical distribution	Coast of California from Santa Barbara County southward and inland 15 or rarely 40 miles; Baja California, Mexico.	California from Newhall to San Bernardino and the area east of Temecula; Los Angeles, San Bernardino and Riverside counties; low elevations; coastal side of the mountains.	California from eastern Los Angeles county (near Glendora) to Riverside county; mostly in shade; low elevations; coastal side of the mountains.	California in the San Gabriel, San Bernardino, and San Jacinto mountains, especially the desert sides; higher elevations.	California in the eastern Mojave desert; eastward to southern Nevada, the southern margin of Utah, and northern Arizona (Mohave to Apache and Yavapai counties).

The species, as it occurs today in southern California, consists of remnants persisting in spots protected in one way or another from the effects of land disturbance by man or from fire. Examples are as follows: (1) in washes or on flood plains where growth of grass on the gravelly soil is restricted to patches, and fires do not carry for great distances; (2) under trees along the foothills where one variety, adapted to shade, may not be enveloped in high grasses which may be shaded out; (3) in the mountains away from the greatest disturbance by man. Also in the hybrid swarms of the "occidentalis" types some individuals with essentially the gene combinations of the postulated original populations still persist.

The nearest relatives of this species are *Opuntia macrorhiza* Engelm. of the the southern Rocky Mountains and the Great Plains and *Opuntia compressa* (Salisb.) Macbr. of the eastern half of the United States. *Opuntia phaeacantha* Engelm. is less closely related.

A. Var. littoralis (Table 1)

Sandy or rocky soils of hills, beaches, and bluffs at 10 to 500 feet (3-150 m) elevation. Disturbed areas of the California Chaparral or coastal (natural or induced) grasslands. Southern California on the islands and along the coast and in low valleys up to 10 or 15 or sometimes 20 to 40 miles inland (as at Pomona and Fullerton). Santa Barbara County to San Diego County. Baja California, Mexico.

This is not the *Opuntia littoralis* of authors, which is, for the most part, *Opuntia oricola* Philbrick. However, this plant and *Opuntia semispinosa* Griffiths have been included in *Opuntia littoralis* as interpreted by some authors.

Opuntia Engelmannii Salm-Dyck var. *littoralis* Engelm. in Brewer & Watson, Bot. Calif. **1:** 248. 1876. *Opuntia Lindheimeri* Engelm. var. *littoralis* Coulter, Contr. U. S. Nat. Herb. **3:** 422. 1896. *Opuntia littoralis* Cockerell, Bull. So. Calif. Acad. Sci. **4:** 15. 1905. *Opuntia occidentalis* Engelm. var. *littoralis* Parish in Jepson, Man. Fl. Pl. Calif. 657. 1925. "The second form, var. *littoralis*, extends on the coast from Santa Barbara and the islands in its Gulf *(O. Tittmann)* to San Diego, and southward, *G. N. Hitchcock*." Tittmann's collection from the islands is of fruit alone; his mainland collection produced a much better specimen. The collection by Hitchcock has not been found in the Engelmann Collection or at the University of California (State Geological Survey collection upon which the Botany of California was based) or elsewhere. The following specimen is designated as a lectotype: Santa Barbara, California, *Otto Tittman*, Jan, 1874. Lectotype: MO. The statement of Coulter, *loc. cit.*, is difficult to understand, "Type, *Tittum [Tittman?]* and *Mallinckrodt* of 1874 in Herb. Mo. Bot. Gard." No such collection has been found.

B. Var. **Vaseyi** (Coulter) Benson & Walkington, comb. nov. (Table 1)

Sandy or gravelly soils of rocky hillsides, alluvial fans, and washes in open areas of the chaparral region at 1000 to 2000 or 4500 feet (300-600 or 1350 m) elevation. Disturbed areas in the California Chaparral. Southern California along and near the west and south bases of the San Gabriel, San Bernardino, and San Jacinto moun-

tains from Newhall to San Bernardino and the area east of Temecula; Los Angeles, San Bernardino, and Riverside counties; rare in Orange county.

Opuntia mesacantha Raf. var. *Vaseyi* Coulter, Contr. U. S. Nat. Herb. **3:** 431. 1896. *Opuntia Rafinesquei* Engelm. var. *Vaseyi* K. Schum., Gesamtb. Kakteen 717. 1898. *Opuntia humifusa* Raf. var. *Vaseyi* Heller, Cat. N. Amer. Pl. ed. 2. 8. 1900. *Opuntia Vaseyi* Britton & Rose, Smithsonian Misc. Coll. **50:** 532. Feb. 28, 1908. *Opuntia occidentalis* Engelm. & Bigelow var. *Vaseyi* Munz, Aliso **4:** 94. 1958. "Type in Nat. Herb. Western Arizona. Specimens examined: Arizona (*G. R. Vasey* of 1881, Yuma; *H. H. Rusby* of 1883, Ft. Verde)." The following specimen is designated as a lectotype: Yuma, Arizona, *G. R. Vasey* in 1881. Lectotype: US 62105, photographs POM 175019, NY, US. Isotype: PH. Various authors have followed Britton & Rose, Cactaceae **1:** 146. 1919, in discounting the Arizonan locality as erroneous and in attributing the epithet to his variety because the Vasey collection is clearly of this taxon.

Opuntia Covillei Britton & Rose, Smithsonian Misc. Coll. **50:** 532. Feb. 28, 1908. *Opuntia occidentalis* Engelm. & Bigelow var. *Covillei* Parish in Jepson, Man. Fl. Pl. Calif. 657. 1925. *Opuntia phaeacantha* Engelm. var. *Covillei* Fosberg, Bull. So. Calif. Acad. Sci. **33:** 102. 1934. "Type in U. S. National Herbarium, no. 40,809, collected at San Bernardino, California, by G. R. Vasey in 1891. . . ." Type: US 40809.

Opuntia magenta Griffiths, Rept. Mo. Bot. Gard. **19:** 268. Nov. 9, 1908. *Opuntia Vaseyi* (Coulter) Britton & Rose var. *magenta* Parish in Jepson, Man. Fl. Pl. Calif. 657. 1925. "The type is no. 7876 D. G[riffiths], collected near Redlands, California, May, 1905." Type: US. These plants combine characters of var. *Vaseyi* and var. *austrocalifornica*, but the combinations are much nearer those of the former.

Opuntia intricata Griffiths, Proc. Biol. Soc. Wash. **29:** 10. 1916. "The type bears my collection number 10,372 from near San Bernardino, California, May, 1912." Type: US. Isotype: POM 288599. These plants tend toward var. *austrocalifornica*, but they are not of that variety.

Opuntia rubriflora Davidson, Bull. So. Calif. Acad. Sci. **15:** 33. July, 1916, not *Opuntia rubriflora* Griffiths, Bull. Torrey Bot. Club **43:** 529. Nov. 7, 1916. "Type station Hollywood reservoir. Frequent throughout the San Ferando Valley."

C. VAR. **AUSTROCALIFORNICA** BENSON & WALKINGTON, VAR. NOV. (TABLE 1)

Humilis; articulis elongato-obovatis glaucescentibus, circa 12.5 vel 20 cm. longis, 5-6.2 cm latis; aculeis 0; petalis pallide purpureis.

Sandy soils of washes, but best developed in the shade under trees along the edges of foothills and in canyons at 800 to 2000 or rarely 4000 feet (240-600 or 1200 m) elevation. California Chaparral. Southern California on the coastal side of the mountains in Los Angeles and San Bernardino counties from near Glendora to San Bernardino and Redlands.

Type collection: Sand and gravel, coastal sagebrush (a successional, disturbed) phase of the California Chaparral, just SE of Indian Hill, Claremont, Los Angeles County, California, *Lyman Benson 15132,* June 3, 1953. Type: POM 285263.

D. Var. **Piercei** (Fosberg) Benson & Walkington, comb. nov. (Table 1)

Sandy and gravelly soils of canyonsides, flats, washes, and alluvial fans in the mountains and along the edge of the desert at 1500 or 3000 to 7250 feet (450 or 900-2175 m.) elevation. Mostly in the coastal and desert-edge phases (including the area of junipers and pinyons) of the California Chaparral but also in the lower part of the Sierran Montane Forest. California from the San Gabriel Mountains to the San Bernardino and San Jacinto Mountains; Los Angeles, San Bernardino, and Riverside counties.

Opuntia phaeacantha Engelm. var. *Piercei* Fosberg, Bull. So. Calif. Acad. Sci. **33:** 102. 1934. *Opuntia Covillei* Britton & Rose var. *Piercei* Munz, Man. So. Calif. Bot. 327. 1935. *Opuntia occidentalis* Engelm. & Bigelow var. *Piercei* Munz, Aliso **4:** 94. 1958. "The type . . . Fosberg No. 8637 from Gold Mountain, San Bernardino Mountains, San Bernardino County, Calif., above Baldwin Lake, altitude 2,100 m. approximately." Type: POM 220076.

E. Var. **Martiniana** (L. Benson) L. Benson, comb. nov. (Table 1)

Sandy or gravelly soils of valleys, flats, and mountainsides at the upper edge of the desert and in woodland at 2000 to 6000 or 8000 feet (600-1800 or 2400 m) elevation. Mojavean Desert and Juniper-Pinyon woodland; lower edge of the Rocky Mountain Montane Forest. Southern California in the region of the New York Mountains, eastern San Bernardino County; Nevada in the foothills of the Charleston Mountains, Clark County; Utah along the Arizona border; Arizona from west-central Mohave County to the northern edge of the Kaibab Plateau in northern Coconino County and to Navajo and Yavapai counties.

The variety hybridizes with *Opuntia erinacea,* and it shades into *Opuntia phaeacantha* and *Opuntia macrorhiza.*

Opuntia charlestonensis Clokey, Madroño **7:** 71, *pl. 4, f. C.* 1943. *Opuntia phaeacantha* Engelm. var. *charlestonensis* Backeberg, Cactaceae **1:** 508. 1958. "Known only from hillsides adjacent to Griffith's mine, associated with *Pinus monophylla* Torr. & Frém. and *P. scopulorum* (Engelm.) Lemmon, at an elevation of about 2450 meters, *Clokey 7203, 7592, 8029* (type), *8688, 8770.* Flower, July to August; fruit, September to October." Type: UC 905408. Isotypes: UC 872654, POM 265222, 275346, MO, BM (2 sheets), WILLU, OSC, UO, GH, US 1828521, PH 815139, ILL, BH, F 1120167, MICH (2 sheets), NY. This colony, studied in the field (*L. Benson 15075,* POM, *15076,* POM, *15077,* POM) as well as the herbaria shows, as do some other populations of var. *Martiniana,* a tendency toward inclusion of some characters of *Opuntia phaeacantha* var. *major,* which occurs nearby at lower elevations.

Opuntia macrocentra Engelm. var. *Martiniana* L. Benson, Cacti Ariz. ed. 2. 64. 1950. "Type collection: Kingman Road on the north side of Hualpai Mountain, Mohave County, Arizona, *L. Benson 10169,* March 30, 1940. Type in the Herbarium of *Lyman Benson, Pomona College Herbarium 274107;* isotype, *Herbarium of the University of Arizona.*" Type: POM 274107. Isotype: ARIZ (not found).

HYBRID POPULATION, "OCCIDENTALIS" (OPUNTIA OCCIDENTALIS OF AUTHORS, NOT OF ENGELM. & BIGELOW)

Below is a description summarizing the characters most commonly occurring in the innumerable combinations in the irregular hybrid swarm resulting, according to morphological data and to chemical evidence (Walkington, *ined.*), from interbreeding of *Opuntia littoralis* vars. *Vaseyi* and, to a lesser extent, *austrocalifornica* with mostly the spiny form of *Opuntia Ficus-Indica* (known commonly as *Opuntia megacantha*).

In 1876 Engelmann (in Brewer & Watson, Bot. Calif. **1:** 248) considered the earlier collections from coastal southern California to represent varieties of "*Opuntia Engelmannii*" (i.e., *Opuntia phaeacantha* var. *discata* (cf. above) of California to Texas and adjacent Mexico), and relationship to that taxon is close. Plants of var. *discata* occur along the desert edges of all the southern Californian mountains from San Bernardino County to San Diego County and in the eastern Mojave Desert. Distinction of some plants in the coastal southern Californian hybrid swarms from *Opuntia phaeacantha* Engelm. var. *discata* and var. *major* Engelm. (at higher elevations in the same parts of southern California and eastward to Kansas, Texas, and northern Mexico) is difficult.

Distinction of *Opuntia littoralis* from the *Opuntia phaeacantha* complex is also not wholly clear because acicular spines shade into flattened spines. Thus, segregation must be partly arbitrary, as is all classification.

Suberect or sprawling shrubs, 1-1.5 or 2 m high, 1-4.5 m or much greater in diam; trunk none or when present very short; larger terminal joints markedly to only slightly glaucous, narrowly elliptic, narrowly obovate, or sometimes broadly either one or rhombic, 1.75-4.5 dm long, 1-2.5 dm broad, 2-2.5 cm thick; areoles elliptic, 6 mm long, typically 2.5-4 cm apart; spines in nearly all or all the areoles, each brown or red on at least the lower half or sometimes all white or gray, 4-7 per upper areole, fewer in the lower areoles, spreading or some deflexed, straight or rarely curving, the longer ones 2-3 or 4 cm long, basally 1-1.25 mm broad, subulate, very narrowly elliptic in cross section, not barbed; glochids yellow to brown, 3-6 mm or more long; flower 7.5-11.2 cm in diam, 6.2-8.7 cm long; sepaloid perianth parts with the midribs green and the margins yellow or partly reddish in age, the largest ones cuneate or cuneate-obovate, 0.6-2.5 cm or more long, 0.6-2.2 cm broad, truncate, mucronate, undulate or toothed; petaloid perianth parts yellow to orange-yellow, becoming reddish in age, the largest ones obovate, 3.8-5.5 cm long, 1.9-4.5 cm broad, mucronate, nearly entire; filaments yellow, 12-15 mm long; anthers yellow, about 2 mm long; style greenish, 1.2-1.9 cm long, 4.5-7.5 mm in greatest diam; stigmas about 10, 3-4.5 mm. long, thick; ovary in anthesis not spiny; fruit red to purple, fleshy at maturity, smooth, not spiny, with some glochids, obovoid, 3.8-7 cm long, 2.5-4.5 cm in diam, with the umbilicus shallow but cuplike, maturing and deciduous in the early winter; seeds tan, variable, nearly orbiculate, the embryo-bearing margin from prominent and irregular to narrow and smooth, 3-6 mm long, slightly less broad, 1.5 mm or more thick.

Sandy, gravelly, or partly clay soils of hillsides and valleys, and, to a lesser extent, alluvial fans and washes at 500 to about 3000 feet (150-900 m) elevation. Disturbed or naturally open areas in the California Chaparral. Coastal side of the mountains of southern California from near Glendora, Los Angeles County, to San Bernardino and Riverside counties and, more doubtfully, southward through the interior foothill region to San Diego County.

Opuntia rugosa Griffiths, Proc. Biol. Soc. Wash. **27:** 27. 1914. "The type is preserved under by inventory No. 10,364, and was secured originally near Pomona,

California." According to a letter from David Griffiths to S. B. Parish, Feb. 16, 1916, Parish Botany Library of Pomona College (583. 471 C 113 V.1), "*Opuntia rugosa* I secured on a circuitous trip which I took from Pomona to Claremont." Type: US. Isotypes: POM 285257, 288613, 291217.

2. Opuntia Ficus-Indica (L.) Miller

Trees 3-5 m or more in height; trunk 6-12 dm long, 2-3 dm in diam; larger terminal joints green, broadly obovate to obovate or oblong, 3-6 dm long, 2-4 dm broad, 1.9-2.5 cm thick; areoles narrowly elliptic, 2-4.5 mm long, 3 mm broad, typically 1.9-5 cm apart; spines none, few, or abundant, white or sometimes on some joints tan or pale brown, 1-6 per areole, some spreading, some deflexed, straight, the longer ones 1.2-2.5 or 3.8 cm long, basally about 0.7 or 0.8 mm broad, subulate, flattened, narrowly elliptic in cross section, not barbed; glochids yellow, numerous, early deciduous; flower 7.5-10 cm in diam, 6.2-8.7 cm long; sepaloid perianth parts yellowish with red or green in the mid-portions, ovate-acute to broadly cuneate or cuneate-obovate, 0.8-3.1 cm long, 0.3-1.9 cm broad, acute to truncate or emarginate and mucronate, denticulate or entire or slightly undulating; petaloid perianth parts yellow or orange, narrowly obovate to narrowly cuneate, 2.5-3.8 to 5 cm long, about 1.2-2.6 cm broad, truncate to rounded, sometimes mucronulate, entire or slightly undulate or denticulate, ovary in anthesis with a few later deciduous short spines; fruit yellow, orange, red, or purplish in various strains, fleshy at maturity, edible, spineless or sometimes with spines, 5-10 cm long, 4-8.7 cm in diam, umbilicus low and concave, persistent for several months.

Probably native in Mexico, where numerous horticultural forms (cultivars) exist, as do many hybrids with other species. Two forms are common in cultivation in the warm, relatively dry regions of the Earth and especially in Mediterranean climates. One, known as *Opuntia Ficus-Indica,* is spineless and relatively less variable in other characters; the other, known as *Opuntia megacantha,* is spiny and relatively more variable in other characters. The *megacantha* form may be, as postulated by Griffiths (cf. above) nearer the wild type, the spineless form perhaps having arisen in cultivation. The introduced forms of both types vary from country-to-country probably because of widespread propagation of clones of types introduced by chance, any form having been chosen in Mexico for propagation elsewhere if the fruit was good. For example, the spineless form covering the south face of the Acropolis of Athens differs from that in California, and both differ from the common type in the eastern part of Cape Province and other areas in South Africa. The spiny form in South Africa differs from those in California and in Hawaii. Introduced into the native vegetation sparingly in California, Texas, and Florida.

Cactus Ficus-Indica L., Sp. Pl. 468. 1753. *Opuntia Ficus-Indica* Miller, Gard. Dict. ed. 8. No. 2. 1768.[4] "*Habitat in* America *calidiore.*" This species was not found in the Herbarium of Linnaeus, Linnaean Society, London, or in the Linnaean Herbarium of the Riksmuseum, Stockholm. Choice of a lectotype or a neotype will require further study.

Opuntia megacantha Salm-Dyck, Hort. Dyck. 363. 1834. "Habitat in Mexico." Salm's specimens were not preserved. The choice of a neotype is deferred pending further study.

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[4] Synonyms and types for plants in this area.

Opuntia occidentalis Engelm. & Bigelow, Proc. Amer. Acad. **3:** 291. 1856 (publication in specific rank questionable because of the following statement: "The following may be considered as a subspecies: —"); U. S. Senate Rept. Expl. & Surv. R. R. Route Pacific Ocean. Botany, **4:** 38, *pl. 7, f. 1-2.* 1856. *Opuntia Engelmannii* Salm-Dyck var. *occidentalis* Engelm. in Brewer & Watson, Bot. Calif. **1:** 248. 1876. (Cf. discussion in the introduction.) The following specimen is designated as a lectotype: "Near Los Angeles, Cal.," actually, as indicated above, from near Cucamonga, 43 mi E of Los Angeles in San Bernardino County, *J. M. Bigelow,* March 19, 1852. Lectotype: MO, photographs US, POM.

Opuntia Engelmannii Salm-Dyck in Engelmann, Pl. Lindh. II, Boston J. Nat. Hist. **6:** 208. 1850. "From El Paso to Chihuahua, indigenous and cultivated *Dr. Wislizenus.* No doubt also on the Texan side of the Rio del Norte." The following specimen in the Engelmann Herbarium is designated as a lectotype: "North of Chihuahua, common as high up as El Paso, *A. Wislizenus,* Aug., 1846." Lectotype: MO, photographs POM, NY. This name has been applied to the large, conspicuous prickly pear occurring from the deserts of California (where it has gone under another name, *Opuntia megacarpa* Griffiths, applied to one specialized local variant) to those of Texas. Unfortunately, the type is from a cultivated plant of the "*Opuntia megacantha*" type. The plants described commonly as "*Opuntia Engelmannii*" are *Opuntia phaeacantha* var. *discata,* page 265.

SOME SUBTRACTIONS FROM THE UMBELLIFERAE OF SOUTH AMERICA

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One of the most difficult problems encountered by floristic workers is that of attempting to single out and identify those plants attributed to an area but which may not actually be indigenous to it. These may be casual introductions, or escapes from cultivation, or they may represent a simple confusion of labels in an herbarium. Often it is not possible to tell which.

I. European weeds described as indigenous species. A common weed appearing for the first time in a strange continent is likely to go unrecognized because it was not expected there, and perhaps also because it may not have attained precisely its customary physiognomy under alien conditions. Once it has entered the record, under any name, it is very difficult to extirpate. Often it is represented by a single specimen deposited in a distant institution, and it may never be re-collected in the locale from which it was first reported and described under a new name. Sometimes it may be recognized because it is the sole, or one of the few, member(-s) of a genus not otherwise represented in the area in question.

The list of *Umbelliferae* described from South America contains at least four examples of this type, three of them collected more than a century ago, which have not been successfully relegated to their proper status and which have thus caused an inordinate amount of trouble. They are: *Ligusticum divaricatilobum* Clos, from Chile; *Ptychotis Vargasiana* DC., from Venezuela; *Seseli Gilliesii* Hook. & Arn., from Argentina; and *Seseli pencanum* Phil., from Chile. The first three of these were sought for and studied in European herbaria in 1963; the fourth apparently is not represented from Chile in the institutions visited. These four contrast with some forty species described in a dozen Old World genera, which have been assigned to their proper generic position.

1. *Ligusticum divaricatilobum* Clos. Described in 1847, this is represented solely by the type specimen at Paris, a Gay collection ostensibly made in "CHILI. Prov. de Coquimbo," in 1838, and by its widely distributed Chicago Museum photograph (Fph 37,089). Comparison with European material indicates beyond a doubt that it represents the Old World species *Seseli Libanotis* (L.) Koch. This identification effectively removes the genus *Ligusticum* from South America, since the dozen or so species described in that genus from Chile fall into *Apium* (Reiche, 1899, 1900) and the single Colombian species is attributable to *Niphogeton.* It probably removes *Ligusticum* also from the entire southern hemisphere, since Dawson (1961) has shown that the so-called *Ligusticum* species of New Zealand are actually referable to *Anisotome* Hook. f. Whether or not *Ligusticum divaricatilobum* was actually collected in Chile—it has been reported to be adventive in the eastern United States—is a moot question.

ANN. MISSOURI BOT. GARD. **52**(3): 274-280. 1965.

2. *Ptychotis Vargasiana* DC. This plant was studied in the de Candolle Herbarium at Geneva, where it was at first thought to be referable to *Pimpinella polyclada* Boiss. & Heldr., but with a leafier inflorescence and an evident involucel. However, a careful comparison of the holotypes suggested that while their resemblance was great, the two did not represent identical taxa. Examination of the *Pimpinella* material in the Edmond Boissier Herbarium indicated that *Ptychotis Vargasiana* is actually only *Pimpinella Anisum* L., the cultivated anise. In this connection there is the comment made on this species by Wolff (1927, p. 232): "Hier und da eingeschleppt, auch in Amerika, nach Coulter und Rose im Staat Massachusetts; in Colombien verwildert (Triana n. 4410)." If *P. Anisum* could become adventive in Colombia—we have seen no specimens—it does not seem incredible that it may have escaped in the vicinity of Caracas, Venezuela, as well.

3. *Seseli Gilliesii* Hook. & Arn. This taxon, ostensibly from the Andes of Mendoza, Argentina, has led a shadowy existence. It was first determined by Gillies and Hooker as *Petroselinum sativum* Hoffm.; Bentham later assigned it to *Carum copticum* L. [=*Trachyspermum copticum* (L.) Link], but it did not seem to be satisfactorily placed in *Petroselinum, Seseli,* or *Trachyspermum.* Although the holotype at Kew is notably fragmentary, it now appears evident that *Seseli Gilliesii,* like *Ptychotis Vargasiana,* is nothing other than *Pimpinella Anisum* L. A specimen each from Bolivia (*Pentland 59,* P) and Chile (*Poeppig s.n.,* W) also are referable here. Reiche (1900, p. 120) lists "*Pimpinella Anisum* L., el anis, de la rejion Mediterránea" among the "Umbelíferas Cultivadas" in Chile. It is apparent that a century ago it must have been cultivated from one end of the continent to the other, becoming adventive at various times and places.

4. *Seseli pencanum* Phil. In describing this species, collected near Concepción in central Chile, Philippi remarked, "Los frutos son tan poco desarrolados, que no puede conocer su estructura con seguridad, así que el jénero es dudoso." It still is. Reiche (1899, 1900) suggested that, because of its white-hairy fruit, it should be compared with *Ligusticum divaricatilobum,* and mentioned the frequent confusion of "Coquimbo" and "Concepción" in older botanical literature. When in 1954 I examined the holotype and an istotype at Santiago, I noted that I did not recognize the plant but thought it might be a weedy biennial rather than a perennial native. Some weeks later I searched vainly for the plant in the greatly altered vegetation near Penco, and became even more convinced of its probably ruderal character.

After another fruitless search, this time in European herbaria, I was fortunate to obtain the excellent accompanying illustration (Fig. 1) from my good friend, Dr. Carlos Muñoz Pizarro, of the University of Chile.

The immature fruit, with its distinctive scabrosity and solitary vittae could, I believe, be attributed only to the Eurasian genus *Seseli,* and it thus appears that Reiche may have been considerably nearer the correct solution than I was willing to admit ten years ago.

II. The identity and status of the genus Azorellopsis Wolff. The identity of this "citizen of the Andes mountains of Bolivia" has long been a puzzle, and ap-

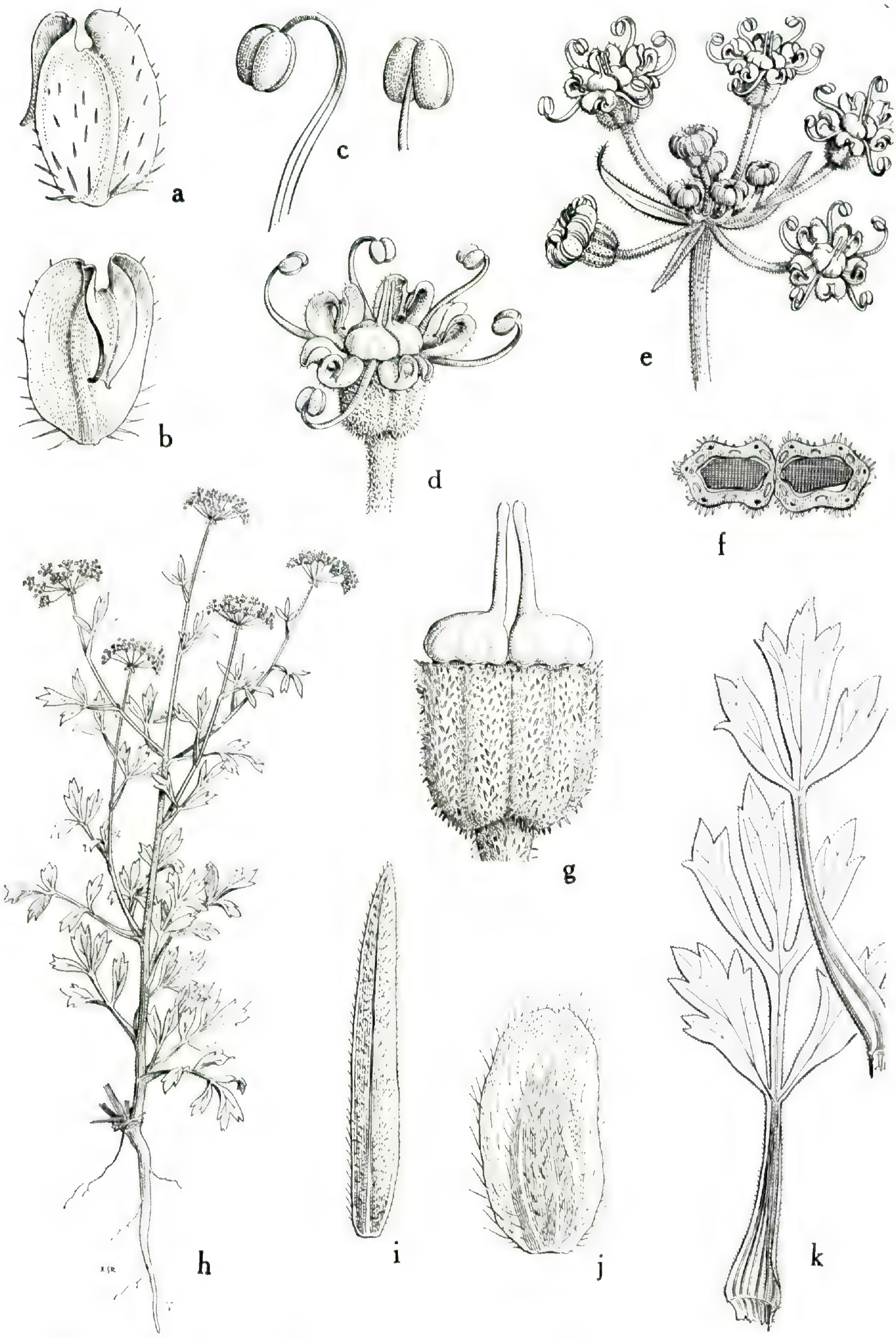

Fig. 1. *Seseli pencanum* Phil. a, b. Petals, ×20. c. Stamen and anther, ×20. d. Flower ×10. e. Flowering umbellet, ×5. f. Transection of immature fruit, ×20. g. Immature fruit, ×20. h. Habit, ×½. i. Involucel bractlet, ×12½. j. Involucral bract, ×12½. k. Leaves, ×2. (All from the type collection, SGO)

parently no one since the original author has commented on its probable affinities. The holotype, a Bridges specimen borrowed from Vienna by Wolff, cannot be found in the herbarium of the Naturhistorisches Museum, and the lack of any collection number for the specimen cited has made it difficult to find a ready substitute for it. It seems unlikely, however, that the Vienna specimen—whatever its fate—would have been the only sheet of that particular Bridges collection. Thus, the best hope seems to be to attempt to discover and identify in some herbarium or herbaria the same Bridges gathering. This was one of the specific objectives of a recent six-months' study trip to some of the principal botanical institutions of western Europe.[1]

But for what kind of a plant should one look? From Wolff's combined generic and specific description (1924) one may visualize the plant he had in hand somewhat as follows: a dwarf perennial cushion-plant with small, thick, obovate, deeply trisect, and sheathing-petiolate leaves, rather few and shortly pedicellate yellow flowers lacking any calyx lobes, and with ovate, acute (but not inflexed) petals. The structure of the inflorescence is problematical, but the ovary consists of two "transversely sub-semiorbicular" (i.e., "D-shaped") carpels attached by their rounded commissural surfaces, with thick dorsal ribs and either the lateral or intermediate ribs shortly winged, and the vittae solitary in the intervals and two on the commissure.

If one then applies this description to the known genera of South American *Umbelliferae,* he finds that the habit restricts him to perhaps the following seven genera: *Azorella, Bolax, Laretia, Mulinum, Pozoa, Niphogeton,* and *Oreomyrrhis.* If the foliage of these genera is examined, the requirement of three-lobed or three-parted leaves eliminates *Laretia, Pozoa,* and *Oreomyrrhis. Bolax* has conspicuous, petaloid calyx lobes (Skottsberg, 1912), so it can be safely eliminated. Finally, the possession of an ovary or fruit with winged ribs surely takes out *Niphogeton* and most probably *Azorella,* for, as noted by Wolff, *Azorellopsis* comprises, "Herbs of the habit of several species of the genus *Azorella,* but the structure of the ovary (dorsal ribs thick, the lateral winged) is distinctly different from the fruit of the *Azorellae.*" (My translation.)

Of the known genera, thus only *Mulinum* remains as a probable candidate, and specimens of this genus were scrutinized with great care for any collections attributable to Bridges. One widespread collection immediately attracted attention: *Bridges 1188* (sometimes given as *Cuming 1188* or *Bridges s.n.*), variously identified as "*Azorella?*", "*Bolax Gilliesii?*", "*Mulinum albovaginatum* Gill. & Hook.," "*Mulinum spinosum* Pers.," "*Mulinum ulicinum* Gill.," or more commonly unidentified. It seems to have been collected in 1841 and, although variously attributed to "Chili," "Coquimbo," and "Colch[agua]", the specimen in the Hooker Herbarium at Kew succinctly states, "Dec. & Jany. Summit of Andes near Volcano of Peteroa" [Curicó, Chile].

[1] The writer wishes to express appreciation for the support of the National Science Foundation (GB 525) and a sabbatical leave granted by The Regents of the University of California. He is grateful also to the directors and staffs of the institutions visited.

Johnston (1928, p. 102) made the following observations on Bridges' itinerary: "I am of an opinion that the hacienda upon which Bridges worked between 1834 and 1841 was in what is now the Province of Curico and that his collections labeled as from the Province of Colchagua in fact came from what is today the Province of Curico. To reach Paso El Planchon, lat. 35° 12′ S., Bridges had to ascend the cordilleras entirely within Curico. Hence there can be little doubt that plants of middle and high altitudes, given as from the Andes of Colchagua, really came from Curico or just within Mendoza across the eastern frontier." He also confirms that "most of the numbers 858 to 1278 were obtained in the Andes or at their base early in 1841." Bridges apparently did not even reach Bolivia until 1844-1845.

Chodat and Wilczek (1902) referred "Cuming, no 1188 (1842)" to their *Mulinum cryptanthum* Clos var. *pulvinaris*. This taxon is similar to the Argentinian *Mulinum Echegarayi* Hieron., judging from an examination of the holotype of the former borrowed some years ago from Lausanne (LAU).

The taxonomy of the genus *Mulinum* is in a state of some confusion, but there is little doubt that the Bridges collection is the taxon known as *Mulinum pauciflorum* Reiche (Fig. 2), which was itself described from "terrenos de arena volcánica de la cordillera de Curicó". This species is widely represented by the Chicago Museum photograph (Fph 3453) of the destroyed Berlin isotype, which bears an unpublished name, and also by the collection, *Werdermann 613*. Very possibly, the Bridges, the Reiche, and the Werdermann collections may all have come from the same place.

There are some discrepancies between the descriptions of *Azorellopsis trisecta* Wolff and *Mulinum pauciflorum* Reiche. The leaf divisions of the latter are said to be "elliptic-oblong" rather than "linear-oblong"; the petals are described as "oblong" rather than "ovate"; and the individual plants are stated to be "dioecious" rather than "hermaphrodite." And perhaps most important is the failure of Wolff to mention the fact stressed by Reiche (1899, 1900) that the leaves are "more or less covered with white hairs", a feature that is quite obvious on herbarium specimens. Wolff had both earlier and later examined material of *Umbelliferae* in or from several of the herbaria containing the Bridges collection, but there unfortunately is no indication that he ever saw or attempted to name any representative of it.

What about the attribution of *Azorellopsis* to Bolivia, where the genus is not known to occur (Foster, 1958)? The Vienna museum has a set of Bridges material lacking any collection numbers or individual data but bearing the over-all designation, "Bolivia leg. Bridges." Among *Umbelliferae* there are included *Gymnophyton polycephalum* (Gill. & Hook.) Clos, probably representing an unnumbered Bridges collection from Mendoza, Argentina; *G. robustum* Clos, probably a duplicate of *Bridges 1371* from Coquimbo, Chile; and *Laretia acaulis* (Cav.) Gill. & Hook., which is perhaps either *Bridges 251* or *Cuming 320*, collections of this Chilean-Argentine endemic found in several herbaria. Since none of these three species is either known from or is very likely to be found in Bolivia, it would not be sur-

prising if the type specimen of *Azorellopsis trisecta* Wolff had been a similarly mislabeled member of the same set.

Unless the holotype unexpectedly reappears or some specimen is discovered that bears Wolff's annotation, the identity of *Azorellopsis* must rest on inferences derived from circumstantial evidence. Although there are discrepancies in the original description, I do not believe any of them are sufficient to negate the reference of the Wolffian genus to *Mulinum pauciflorum*.

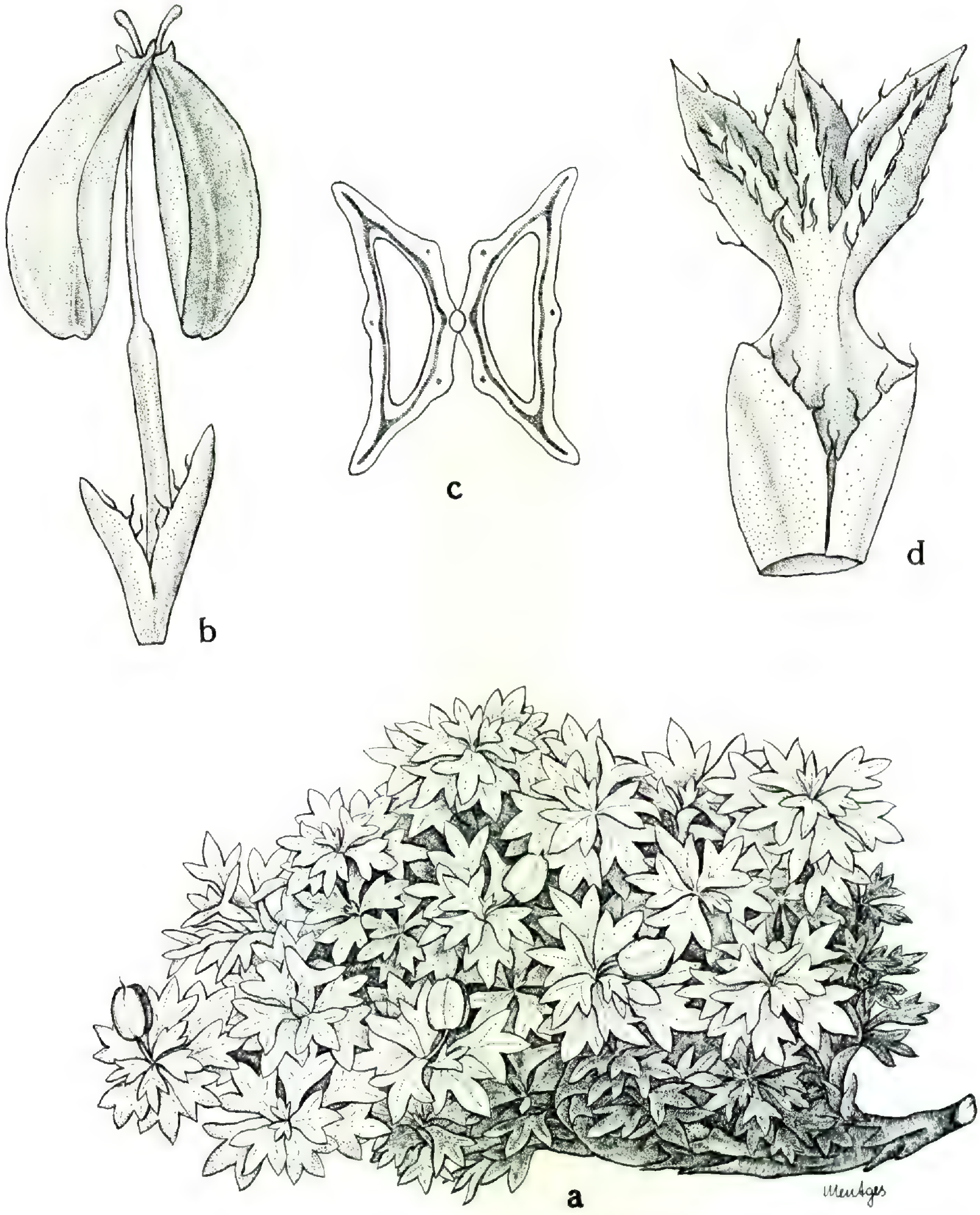

Fig. 2. *Mulinum pauciflorum* Reiche. a. Habit, ×1. b. Fruit, ×5. c. Fruit transection ×7. d. Leaf, ×5. (All from *Werdermann 613*, UC)

Summary

Seseli Libanotis (L.) Koch, Nova Acta Acad. Leop.-Carol. **12:** 111. 1825.

Ligusticum divaricatilobum Clos ex Gay, Fl. Chile **3:** 131. 1847. Based upon *C. Gay*, "CHILI. Prov. de Coquimbo," 1838 (P-Holotype; Fph 37,089 of Paris holotype).

Pimpinella Anisum L., Sp. Pl. 264. 1753.

Ptychotis Vargasiana DC., Prodr. **4:** 109. 1830. Based upon *Vargas*, "circà Caracas" [Venezuela] (G-Holotype).

Seseli Gilliesii Hook. & Arn. in Hook., Bot. Miscel. **3:** 354. 1833. Based upon *Gillies*, "Valle de la Punta de las Vacas, Andes of Mendoza" [Argentina] (K-Holotype).

Additional South American collections: "Bolivie. Chivesivi = Vallée S. de la Paz = alt. 8500 à 12000 = pd. angl.", 1839, *Pentland 59* (P). "Chile bor. Andes de Sa. Rosa" [Aconcagua], *E. Poeppig s.n.* (W).

Mulinum Pers., Syn. Pl. **1:** 309. 1805.

Azorellopsis Wolff, Repert. Nov. Sp. **19:** 312. 1924.

Mulinum pauciflorum Reiche, Anal. Univ. Chile **104:** 803. 1899; Fl. Chile **3:** 82. 1900.

Azorellopsis trisecta Wolff, Repert. Nov. Sp. **19:** 312. 1924. Based upon *Bridges*, "Bolivia."

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THE STATUS OF THE GENERAL SYSTEM OF CLASSIFICATION OF FLOWERING PLANTS[1]

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Introduction

The Linnaean system of plant classification, which arranged all the genera into some 24 admittedly artificial classes, was such a great improvement over its predecessors, and was so universally adopted, that eventually it outlived its usefulness and became a handicap to further taxonomic progress. In the 9th decade after the appearance of the Species Plantarum, distinguished botanists such as W. J. Hooker (1) in England and Amos Eaton (2) in America were lamely defending their continued use of the familiar Linnaean system, instead of one of the several purportedly natural systems that had been put forward in its place. Within another few years the Linnaean system simply vanished.

The well known and very useful Englerian system is having a similar history. Now moribund, it continues to be used because people are familiar with it, and because there is as yet no agreement on a successor. The most recent [1964] edition of the Engler Syllabus (3) is noteworthy, among other respects, in that it marks the recognition in Engler's home institution that his system must be so extensively modified as to lose its identity. The monocots are placed after the dicots in this edition and are completely reorganized, with the *Alismataceae* coming first in the sequence. Only a few families of dicots, such as the *Cactaceae* and *Curcurbitaceae,* are moved far from their accustomed place, but there are numerous notes indicating that a change in the position of this or that family will be necessary in order to associate it with its nearest relatives. Abandonment of the *Amentiferae* and recognition of the Ranalian complex as the primitive group in the angiosperms are clearly forecast in this edition of the Syllabus.

The critical weakness of the Englerian system is that it fails to recognize the significance of reduction and therefore tends to equate the simple with the primitive. As a result, the *Amentiferae* are considered to be primitive among the dicots, and the *Typhaceae* among the monocots, and no real connection is seen between the monocots and dicots. By 1926 Engler (4) had realized that the flowers of the *Amentiferae* are simplified rather than primitively simple, and he argued that their extreme reduction indicated the great antiquity of the group. Such an argument misses the whole point of a phylogenetic system. An essential requirement of any phylogenetic system is that one start with the groups which are least modified from the ancestral prototype, rather than with those that have undergone the most change. All groups are of equal age, if one takes in all the ancestors as well as the members of the group. It is only if one bases concepts of age on the members that

[1] Adapted from an address delivered to the Botanical Section of The American Association for the Advancement of Science, at Montreal on December 29, 1964.

Ann. Missouri Bot. Gard. **52**(3): 281-303. 1965.

would actually be referred to a particular group that groups differ in age and a phylogenetic system becomes possible.

We should note at this point that the now widespread dissatisfaction with the Englerian system does not relate primarily to the arrangement of genera into families. Some disagreement on the limits of families is inevitable, and the problem of lumping or splitting will always be with us, but no one wants to reshuffle the genera into a basically different set of families. The dissatisfaction relates instead to the arrangement of families into orders, and to the concepts of relationships among the orders, including how these may best be arranged in a linear sequence. Such arrangements necessarily depend to a large extent on one's concepts of the nature of the primitive angiosperms and the evolutionary trends that have affected the structure and chemistry of their decendents.

Significance Of The Fossil Record

One of the greatest problems in any consideration of the evolutionary relationships among the angiosperms and the ancestry of the group is that the fossil record tells us so little. So far as the fossil record is concerned the angiosperms might have originated by special creation early in the Cretaceous period as a set of several woody families occurring in various parts of the world and having no connections to any other groups. Several Jurassic and Triassic fossils have at one time or another been considered to be possibly angiospermous, but some of these have been shown to be gymnospermous, and the others are doubtful at best (5).

Perhaps the most interesting preCretaceous fossil that might prove to be an angiosperm is *Sanmiguelia* (6), a palm-like plant from Triassic deposits in Colorado. The fossils consist only of leaf-impressions, with no cellular detail. They do indeed look like parts of palm leaves, and if they had been found in Cretaceous or later deposits they would probably pass as palms without serious question. However, they are also much like cycadophyte leaves, and if there were no such things as palm trees these fossils would doubtless be considered to be cycadophytes. Palms are not usually considered to be very primitive among the angiosperms; indeed they are one of the more highly specialized groups. If *Sanmiguelia* is really a palm, some re-thinking of our concepts may be in order, but without flowers, fruit or wood its status as a palm must rank as an interesting possibility rather than a fact or even a probability.

The question of the affinities of *Sanmiguelia* points up one of the most pervasive problems in the study of fossil angiosperms. Aside from pollen grains, most of these fossils are mere leaf-impressions. Fruits, when present, are seldom attached to the leafy branches and rarely show enough structural detail to be identified without a great deal of inference, although a few kinds, such as the double samaras of maples, are easy enough to recognize. Fossil flowers are rare and do not generally show the structures needed for accurate identification. Students of vertebrates are fortunate in that the parts most likely to be fossilized (the bones) are also the parts that tell the most about the nature and taxonomic affinity of the animal. Angiosperm taxonomists are in the reverse position. The parts most likely to be

fossilized (leaves) tell us little that can be relied on. All taxonomists are aware of the difficulty of identifying sterile material, and the difficulty is compounded when one has not the plant itself, but merely an imprint of part of it. A purported fossil cactus was recently reinterpreted as the rhizome of a member of the *Cyperaceae* (7), and a long list of equally startling reinterpretations could be cited.

Even when an angiosperm fossil can be satisfactorily identified, it merely documents the existence of a particular group at a particular time. The vegetative diversity among and within the families of angiosperms is far too great, and too bewildering, to permit accurate recognition, on vegetative characters, of forms transitional between the modern groups. Some Cretaceous leaf-impressions of *Sassafras* are so characteristic that it is hard to question their identity, but what do these fossils tell us about the relationships of *Sassafras?* Nothing.

Pollen grains, both modern and fossil, can often be identified, at least to the family, more accurately than leaves. A great deal of information about fossil pollen has now been accumulated, but most of it is locked away in the files of oil companies and is not readily available to the scientific fraternity. From Elso Barghoorn (5, 8) I learn that much of the older fossil angiosperm pollen cannot be certainly assigned to any existing family, and that pollen which can be identified as representing herbaceous families is virtually nonexistent before the Miocene period. Even such wind-pollinated groups as the *Chenopodiaceae* and some of the *Compositae* do not show up until the Miocene, and the presence of herbaceous pollen is now coming to be looked on as a marker of Miocene or post-Miocene deposits. This is in accord with conclusion which most taxonomists have accepted on other grounds that the herbaceous habit in angiosperms is secondary rather than primitive.

Since the fossil record tells us so little, our concepts of relationships among the angiosperms must be based largely on comparisons of living species. This does not put us in so difficult a position as one might imagine. It is becoming increasingly plain that the number of potential schemes which will adequately provide even for the information now available, without serious internal contradictions, is not large; and the range of choice becomes increasingly more restricted as more information becomes available. It is the now obvious contradictions in the Englerian system which have stimulated botanists to strive to create a better one. New information is needed to help solve many of the problems, but even the presently available evidence imposes narrow limits on the range of potentially acceptable schemes, and no scheme has yet been devised which properly provides for all the information now available.

Ancestry Of The Angiosperms

Before getting to the main business of the general system itself, we might profitably consider the probable ancestry of the angiosperms. Here in our discussion we are faced with the common pedagogical dilemma that everything ought to come before everything else. Our thoughts on the ancestry of the angiosperms are necessarily conditioned to some extent by our beliefs on the relationships and evolutionary trends within the group. A potential ancestor should be something from which

the primitive characters within the angiosperms could reasonably have been derived, and the possible connection to the angiosperms should be with the more primitive families rather than with the more advanced ones.

Modern thinking on the ancestry of the angiosperms is based on what we might call the Ranalian concept of angiosperm evolution, to which we will refer again after a bit. The difficulties in finding a potential ancestor for the angiosperms are not lessened under any other concept of angiosperm phylogeny to which I have been exposed; instead they are magnified to the point of desperation. Here again we see that the available information imposes severe limitations on the range of concepts which can be seriously entertained. The fact that under the Ranalian concept we do have a possible ancestor for the angiosperms is one more piece of the theory that fits the other pieces, thus increasing our confidence that the theory is basically sound.

If I may be permitted one more digression, I should point out that when I speak of modern thinking, or a consensus, I am not unaware that it is easy to mistake one's own thoughts for the mainstream of opinion. There is certainly no lack of papers expressing ideas contrary to what I conceive to be the general opinion about angiosperm evolution. The recently published gonophyll theory (9) of Melville is an example. I do not accept the gonophyll theory, and I do not believe that most other taxonomists do. One of my friends commented, in referring to this and another novel interpretation of floral morphology, that "Carpels and stamens can be seen; gonophylls have to be imagined; and anthocorms offend the imagination." The paper I am presenting here is a mosaic and partial blend of my personal opinion and an attempt to assess the general opinion; I hope it is fairly plain which is which, or at least which I conceive to be which.

It is now generally agreed that the angiosperms are probably derived eventually from the seed ferns. The evidence for this conclusion has been presented by Takhtajan (10), among others. All other groups that have been suggested as possible ancestors can be ruled out on seemingly adequate grounds.

The *Chlamydospermae* (*Gnetales*, sens. lat.) were once taken seriously as possible ancestors of the angiosperms, and indeed *Gnetum gnemon* could pass for *Coffaea arabica* when in sterile condition, but the reproductive morphology of the *Chlamydospermae* is all wrong for a potential ancestor of the angiosperms (especially under the Ranalian concept), and the idea has been generally abandoned. Even the gnetalean vessel, once seen as a possible link to the angiosperms, is now seen as a conclusive barrier to any such relationship. Bailey (11) and others have pointed out that the vessels in the *Gnetales* evidently originated from tracheids of the coniferophyte type with circular bordered pits, quite different from the fernlike (and cycadlike) scalariform tracheids that gave rise to the angiosperm vessel.

Even the seed ferns present some difficulties as possible ancestors to the angiosperms. It is now coming to be believed, on the comparative morphology of the angiosperms themselves, that the primitive position of the angiosperm ovule is on the upper (adaxial) surface of the carpel, instead of on the margins as was once believed. In the seed ferns the ovules were generally marginal or on the lower

(abaxial) surface of the leaves, but at least one seed fern, *Emplectopteris* (12) is generally interpreted as having the ovules on the upper surface, so perhaps there is no problem here after all. It is still a long ways, morphologically, from any known seed fern to any known angiosperm, but, unlike all other groups of gymnosperms, the seed ferns have the characters from which those of the angiosperms could logically have been derived. If anything should turn up to rule out the seed ferns as possible ancestors, then I suppose the angiosperms will have to hang on an evolutionary skyhook until more evidence is available or old evidence is reinterpreted.

Primitive Characters and Evolutionary Trends

Nearly all modern systems of angiosperms fall into the deCandolle (13)—Bentham and Hooker (14)—Bessey (15) tradition that the Ranalian complex is primitive and that aggregation, fusion, reduction, and loss of parts are prominent trends in floral evolution. This is what we referred to earlier as the Ranalian concept of evolution. It is further generally agreed that the ancestral home of the angiosperms is in the moist tropics, that the woody habit is primitive, and that vessels have evolved from tracheids several times independently within the angiosperms. Inasmuch as *Austrobaileya* has a gymnospermous type of phloem (16), without companion cells and with scattered sieve areas rather than a terminal sieve plate on the sieve elements, it also appears that typical sieve tubes and companion cells evolved after the angiosperms had already differentiated from their gymnospermous ancestors.

The characteristic angiosperm stamen, with slender filament and terminal anther, evidently evolved in several parallel lines within the angiosperms from a broad, flat, sessile microsporophyll with sporangia embedded in the blade. This primitive type of stamen still exists in *Degeneria,* and stages in the evolution of the typical stamen from it are shown in various members of the Ranalian complex.

Even the closed carpel, which we customarily think of an definitive of the angiosperms, evidently originated several times among the primitive members of the group (17). Some species of *Drimys,* in the family *Winteraceae,* a member of the Ranalian complex, have thin, unsealed carpels that are merely folded along the midrib, the ovules being borne on the two inner surfaces of the folded carpel. The carpels of some species of *Bubbia (Winteraceae),* and of *Degeneria,* are very much like the *Drimys* carpels mentioned above, except for being abaxially somewhat deformed. In these genera a mat of tangled hairs running the length of the carpel serves as an elongate stigma on which the pollen grains germinate. Stages in the development of the typical simple pistil, with closed ovary, style, and terminal stigma are still preserved among various living members of the Ranalian complex.

It thus appears that vessels, true sieve tubes, companion cells, the angiospermous stamen, and the closed carpel, all of which are considered as typical angiospermous features, arose *within* the angiosperms. Furthermore, each of them arose several times in a series of more or less closely related parallel evolutionary lines, and in any one line they did not all evolve at the same time. Thus *Degeneria* has unsealed carpels and laminar stamens, but also has vessels, sieve tubes, and

companion cells; *Austrobaileya* has vessels and closed carpels, but lacks sieve tubes and companion cells; *Drimys* has unsealed carpels and lacks vessels, but does have sieve tubes and companion cells. Other combinations of ancestral and typical angiospermous characters occur in other members of the Ranalian complex.

Three features remain as characters which are largely or wholly restricted to angiosperms and which are uniformly developed in primitive members as well as in most or all of the more advanced members of the group. These are 1) germination of the pollen at some distance from the ovule; 2) the extreme reduction of the female gametophyte; and 3) double fertilization, with the attendant development (or at least initiation) of a triploid or polyploid endosperm. This last character fails in certain orchids (18), and of course in many apomicts in various families, but these exceptions are obviously special cases which have no bearing on the evolutionary history of the angiosperms as a whole.

It would be rash to assume that these three characters, on whose evolutionary history we have so little evidence, arose in any different phyletic pattern from the characters previously discussed. Double fertilization and the extreme reduction of the female gametophyte are probably phyletically linked, but the linkage need not have been a tight one. Reduction of the gametophyte is a general trend throughout the vascular plants, and further stages in the reduction of the female gametophyte, beyond the typical 8-nucleate stage, are to be seen within the angiosperms in various families which are not very closely related to each other. It seems likely that the evolution of the 8-nucleate embryo sac from the ancestral multicellular female gametophyte followed a similar pattern of parallelism.

Germination of the pollen grain at a point removed from the ovule is restricted to angiosperms, among living plants, but it also occurred in the fossil *Caytoniales*. This character is obviously correlated with the enclosure of the ovules, so that the pollen cannot land at the micropyle. Since we have seen that the evolution of the closed carpel occurred in a series of parallel lines, it seems reasonable to assume that pollen germination followed a similar evolutionary pattern.

Thus it appears that there probably never was an original angiosperm, from which all other angiosperms are descended. Rather we must visualize an evolving group of pteridosperms which broke up into a number of more or less parallel lines in which similar sets of evolutionary changes took place in only loose correlation with each other. There was no inherent point in time or morphological change at which we could say that *now and only now* the group has become angiospermous. The boundary must instead be arbitrary, and wherever this arbitrary boundary of angiospermy may be established, the several lines probably did not all cross it at precisely the same time.

Simpson, with abundant fossil evidence to back up the comparison of living species, has visualized a similar pattern for the origin of mammals (19). There was no original mammal, from which all other mammals are descended. Before one can trace all the mammals back to a common ancestor, one has not a mammal but a reptile. All the phylads which evolved from reptiles into mammals came from the same general taxonomic part of the reptiles, however, and there was a loose correlation in time as well.

I have elsewhere (20) pointed out that this sort of parallelism is a rather general evolutionary pattern, and that our taxonomic thinking should be adjusted to provide for it. Taxonomy can provide only a somewhat muddy reflection of phylogeny. The phyletic concept, and the monophyletic requirement for a natural taxonomic group, are useful and indeed necessary to a proper taxonomic system, but the monophyletic requirement must be interpreted broadly or it will get us into a lot of unnecessary trouble. In order to be natural and taxonomically acceptable, it is only necessary that a group fall somewhere toward the monphyletic end of the continuous scale which connects the strictest monophylesis with the most utter polyphylesis. Simpson (19) has proposed the useful rule of thumb that if all the members of a group of a given taxonomic rank are derived from another group of lesser taxonomic rank, that is a sufficient degree of monophylesis for taxonomic purposes. The decision as to whether a proposed group is sufficiently monophyletic to be taxonomically acceptable will frequently require the exercise of personal judgment, but the necessity for such judgments is no stranger to taxonomy; indeed they cannot be avoided.

Parallelism is conspicuous at all taxonomic levels within the angiosperms, as well as being thoroughly involved in their origin. All of the common characters or specializations, and most of the rare ones, have arisen independently more than once, most of them several or many times, so that the occurrence of a particular character in two different families provides no guarantee of their close relationship. Even such a rare character as entomophagy has evidently arisen quite separately in the *Sarraceniales* and the *Lentibulariaceae.* One of the most frequent statements in Takhtajan's excellent review (21) of the evolutionary trends in individual characters of angiosperms is something to the effect that "this change has taken place repeatedly in the most diverse groups." Perhaps the most important weakness of Bessey's system (15) is that he failed to recognize how often perigyny and epigyny have arisen from hypogyny. The devastating error in Hutchinson's system (22, 23) is his assumption that there was an early and fundamental dichotomy between woody and herbaceous angiosperms.

This all-pervasive parallelism is indeed the chief obstacle to the formulation of a satisfactory general system. Just when the perception of a series of similarities between two groups leads us to postulate a close relationship between them, something else turns up to suggest that they are not so closely related and that the similarities are due to parallelism. I have pointed out elsewhere (20) that parallelism itself provides some evidence of relationship, because it reflects the realization of initially similar mutative and evolutionary potentialities, but the complex set of overlapping parallelisms in the angiosperms is difficult to understand and easily gives rise to conflicting interpretations. In establishing our concepts of relationships, we are going to have to pay more attention to what Thorne (24) has called non-missing links. It is the more primitive members of a group which give the best clues to its ancestry.

Another common problem in angiosperm taxonomy is that the characters marking the major groups, at the level of family and order, are usually difficult or impossible to correlate with ecologic niches and survival value. Most modern

students of evolutionary theory maintain that the correlations must exist, even if they are difficult to demonstrate; they cannot conceive of evolutionary trends or taxonomic groups that are not shaped primarily by selection, although they admit that the frequency of a particular mutation will differ in different groups. I have (20, 25) expressed the contrary opinion that evolution at the familial and ordinal levels in angiosperms is to a large extent shaped by the supply of mutations rather than by natural selection, and that many of the taxonomically important characters by which the families and orders are recognized have little or no selective significance. Regardless of who is right about this, the fact remains that no systematic attempt to find and elucidate such correlations for the Englerian or any other comprehensive system has come to my attention. The makers of systems have proceeded as if most of the families and orders of angiosperms had no selective significance; so far as the printed record shows, they have simply ignored the question.

Still another very serious obstacle to the development of a satisfactory general system is that the characters which mark the families and orders are subject to frequent exception. Exceptions to the ordinal characters are indeed so numerous that it is difficult to find criteria sufficiently stable for even the most loose and general characterization of the groups. Some botanists have gone so far as to say that the orders of angiosperms can be defined only by the list of families to be included. This may be an unnecessarily pessimistic position, but it does point up the difficulty.

The difficulty in characterizing families and orders may well be related to the seeming (or actual) lack of close correlation of many of the families and orders with well defined ecologic niches. If the taxonomically critical characters are not of great importance to the organism, or if the evolutionary barriers between different ecologic niches are minimal, then happenstance mutations affecting the critical characters will not be rigorously selected against. Differences in the corolla, for example, are very useful in characterizing the families and orders, yet many of the larger families have apetalous genera or species.

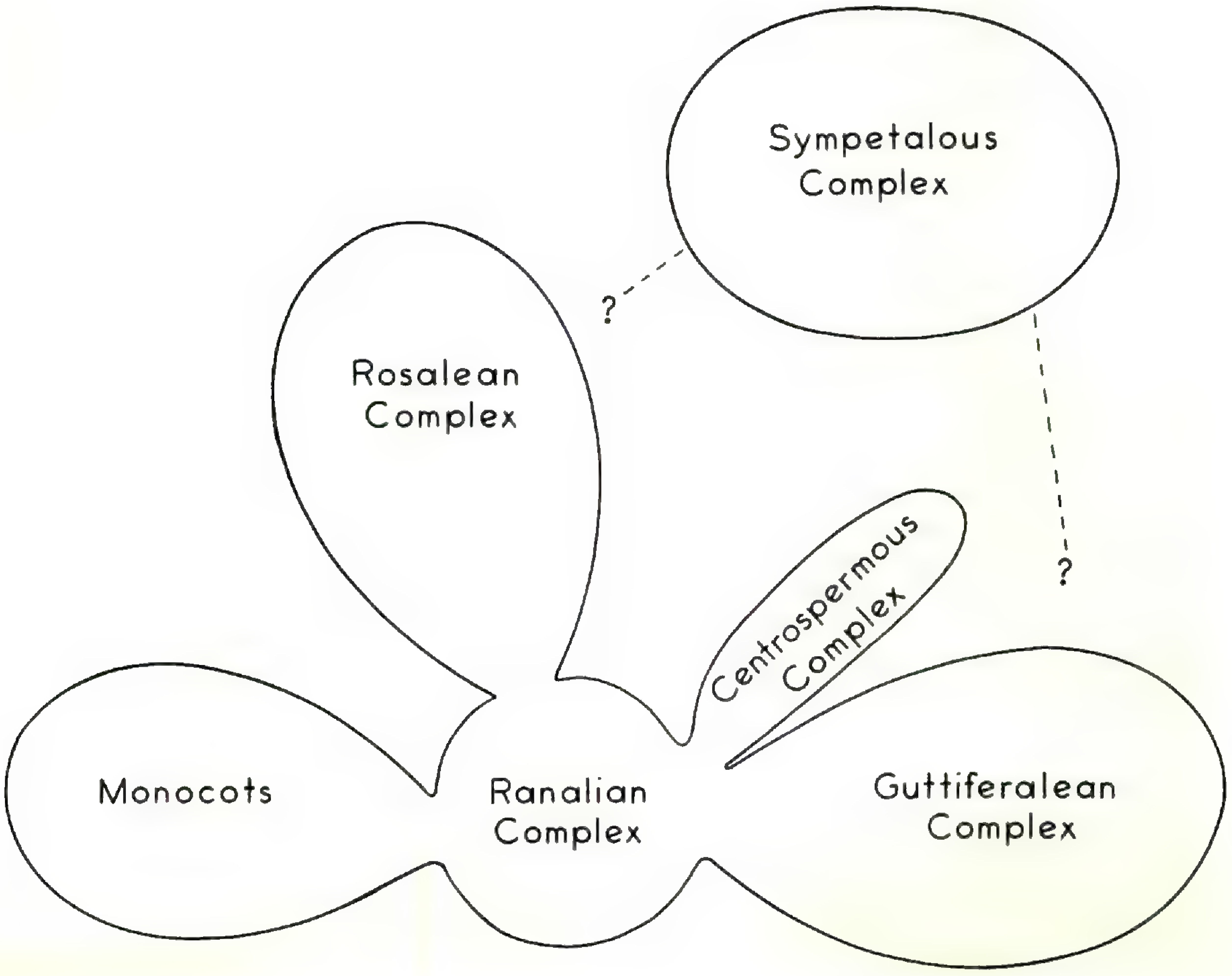
In spite of the difficulties, real progress is being made. We have already noted that any acceptable new system must fall within the deCandolle—Bentham & Hooker—Bessey tradition and must be largely shaped by what we have called the Ranalian concept of angiosperm evolution. There is also a fairly general agreement on a number of the particular features in which such a system must differ from the traditional Englerian system.

As we have noted, there is a very large measure of agreement on how the genera of angiosperms should be assorted into families. A few problematical genera are kicked around from one family to another, and of course we will always have the problem of splitting versus lumping, but no one feels the need for a wholesale reshuffling of genera into families of different limitations constituted on different grounds. Changes in our concepts of families during the present century have been relatively minor. The current Engler Syllabus, to which we have already referred, is as good a standard for family limits as any, and it has the merit of providing a full description for each family.

The arrangement of families into orders, and the concepts of relationships among the orders, are as unsettled and controversial as the arrangement of genera into families is stable. Within the limits of what we have called the Ranalian concept of angiosperm evolution there is still room for a great variety of systems, and it may yet be some time before a generally acceptable complete system emerges. Hutchinson's system of monocotyledons (22, 23) is very respectable, although I would prefer to see the families and orders more broadly defined. Hutchinson's scheme of dicotyledons, on the other hand, is hopeless, the most recent version (23) even more so than the earlier one (22) because now he has more nearly followed through the implications of his assumption that there was an early and fundamental dichotomy between woody and herbaceous angiosperms. Several years ago I published an outline scheme for the dicotyledons (26), to which I still adhere for the most part, although there are some things that need to be changed. Probably the best complete system which attempts to provide for all the families of both monocots and dicots is that of Takhtajan (21), but I believe it is still in need of substantial modification. I am looking forward to seeing the system that Thorne is working on, but I know little about what will be in it.

Dicotyledons

A rough general idea of the probable relationships among the major groups of dicots may be had by visualizing two major and several minor lines of development from the Ranalian complex. One major line leads to the *Guttiferales* (with the



Dilleniaceae as a connecting link), and thence to the *Violales* (*Parietales*), *Malvales, Ericales,* and *Ebenales.* In this line the stamens usually (always?) develop in centrifugal sequence, if there are enough stamens for any sequence to appear. The *Caryophyllales* (*Centrospermae*) and their allies likewise have centrifugal stamens and may be a basal branch from this line, or they may be a separate minor line of their own from the Ranalian plexus. The second major line from the *Ranales* leads to the *Rosales* and thence to such mainly compound-leaved groups as the *Sapindales, Geraniales,* and *Umbellales.* Several simple-leaved groups such as the *Myrtales, Celastrales, Linales, Polygalales,* and *Cornales* also relate to the rosalean line. In this line the stamens are always, so far as known, centripetal. A third large group consists of the orders *Gentianales* (*Contortae*) through *Asterales* in the Englerian sequence, with the exception of the *Cucurbitales,* which relate to the *Violales.* The affinities of this third group, which includes most but not all of the traditional *Sympetalae,* are still doubtful, although they must of course be derived eventually from the Ranalian complex.

The possible taxonomic significance of centrifugal stamens was first pointed out by Corner (27). It is generally conceded that the centrifugal sequence is secondary, being derived from the standard centripetal sequence, but the centrifugal type occurs in *Drimys* (28), which on other grounds is among the more primitive genera of angiosperms. Aside from *Drimys,* all the groups known to have centrifugal stamens fall into only two circles of affinity, the Dillenialean-Guttiferalean-Parietalean-Malvalean complex, and the centrospermous complex, and we have noted the possibility that these two complexes are themselves closely related. Determining the sequence of maturation is not always easy, however; often it is necessary to make long-sections of unopened buds. We should not be surprised if further studies tend to blur what now seems to be a fairly clear pattern.

The *Canellaceae,* which have customarily been referred to the *Parietales* because of their compound ovary and parietal placentation, are now generally admitted to belong in the Ranalian complex, or to be derived directly from it, which amounts to the same thing in terms of phylogenetic relationships. This is one of the few families of dicots to be actually moved in the new Engler Syllabus, where it appears after the *Myristicaceae* in the order *Magnoliales.*

Hutchinson's suggestion (22) that the *Aristolochiaceae* are derived from something in the Ranalian complex has meet with general approval. Here we have one of Thorne's nonmissing links: *Saruma,* in the *Aristolochiaceae,* has well developed petals as well as sepals, and has essentially free carpels.

It is now admitted by all that *Paeonia* does not properly belong in the *Ranunculaceae* and must be treated as a family by itself. The necessity to remove *Paeonia* from the *Ranunculaceae* was pointed out as long ago as 1908 by Worsdell (29), who based his conclusion largely on anatomical grounds. In 1941 Gregory (30) found *Paeonia* to be cytologically anomalous in the *Ranunculaceae.* In 1955 Hammond (31) was unable to relate *Paeonia* to anything in the *Ranunculaceae* by his serological tests, although he did find that *Hydrastis* and *Glaucidium,* whose position in the family has been questioned, reacted with some other members of the *Ranunculaceae.* In addition to its persistent, leathery sepals and prominent

disk, *Paeonia* differs morphologically from the *Ranunculaceae* in having centrifugal stamens.

It is becoming customary to associate the *Paeoniaceae* and *Crossossomataceae* with the *Dilleniaceae* in an order or suborder of their own. This was first suggested, so far as I know, by Camp (32) in 1950. It has been almost universally adopted since then, including in my own work, but I am not sure that the situation is as clear as the developing consensus would suggest. Camp's grouping is very probably correct, but I don't think of it as being one of the firmly established parts of the system.

The order *Rhoeadales* has seemed to be one of the more natural orders, but recently we have been seeing repeated suggestions that it should be divided into two: the *Papaverales*, containing only the *Papaveraceae* and *Fumariaceae*, and the *Capparidales*, containing the remaining families, i.e. the *Capparidaceae*, *Cruciferae*, *Resedaceae*, *Moringaceae*, and *Tovariaceae*. Biochemical (33) and serological (34) evidence both seem to support this separation. The *Papaverales* are then seen as derived directly from the Ranalian complex, whereas the *Capparidales* are regarded as more nearly allied to the *Guttiferales* or *Violales*. I am dragging my feet a little on this one, and I would particularly like to see a careful investigation of the *Tovariaceae*, which have endospermous seeds like the *Papaverales*, and which have the placentae so deeply intruded that the placentation at first appears to be axile. Meanwhile it will perhaps do no harm to recognize the two orders as distinct, even if it eventually turns out that they are more closely related than now appears.

The close relationship among the *Guttiferales*, *Violales*, *Malvales* and *Capparidales* is now generally admitted, as is the transitional position of the *Dilleniaceae*, which are obviously part of the Ranalian complex, and equally obviously allied to the *Guttiferales*. The cucurbits have also become noncontroversial, and in the new Engler Syllabus they are moved to a position adjacent to the *Violales*. The only remaining difference of opinion is whether they (the cucurbits) should be submerged in the *Violales* or maintained in a separate order which is considered to be closely related to and immediately derived from the *Violales*.

Some of the traditional *Sympetalae* appear to be derived from the *Guttiferales*. Most obvious among these are the *Ericales*, which include both sympetalous and polypetalous members, even in such a relatively homogeneous group as the *Monotropoideae*. The small families *Clethraceae* (*Ericales*) and *Cyrillaceae* (*Guttiferales*) are sometimes seen as forming a near-connection between the two orders, but the position of the *Cyrillaceae* themselves is not wholly agreed on. The new Engler Syllabus retains the *Cyrillaceae* in the *Celastrales*, while commenting on their probable relationship to the *Guttiferales* and *Ericales*. Even without the *Cyrillaceae*, the *Clethraceae* are a good bridge between the two orders. The relationship of the *Clethraceae* to the *Ericaceae* has been evident to all, but their generally morphology is also consistent with a placement in the *Guttiferales*, a position which is also suggested by the pollen (35) and the nectaries (36).

The *Empetraceae*, with distinct or no petals, are now widely admitted to be reduced relatives of the *Ericaceae*, which they closed resemble in appearance. The *Empetraceae* are another of the small list of dicot familis which are moved to radi-

cally new positions in the new Engler Syllabus, where they are relegated to the *Ericales*.

The *Lennoaceae*, a small group of nongreen root-parasites, were formerly included in the *Ericales*. More recent studies (35, 37, 38) indicate a position near the *Hydrophyllaceae* and *Boraginaceae*, and this is another family which has actually been moved in the new Engler Syllabus.

The *Ebenales* are now generally believed to be derived from the *Guttiferales* (*Theales*), as postulated by Copeland (39), although the evidence may not be so strong here as it is for deriving the *Ericales* from the *Guttiferales*.

The *Caryophyllales* (*Centrospermae*) consist of a relatively homogeneous core of 9 families (*Phytolaccaceae, Nyctaginaceae, Aizoaceae, Portulacaceae, Basellaceae, Chenopodiceae, Amaranthaceae, Molluginaceae, Caryophyllaceae*), plus some certain (*Cactaceae*) and possible (*Polygonaceae, Didiereaceae, Batidaceae, Thelygonaceae*) allies which are sometimes but not always included in the group. The core families have a series of embryological features in common, which have been enumerated in the new Engler Syllabus, among other places. Notable among these features are the massive nucellus which develops into a perisperm in the seed, the double integument with the inner one forming the micropyle, trinucleate pollen, and peripheral embryo which tends to curve around the perisperm. When the stamens are numerous, as in the *Aizoaceae* and some *Portulacaceae*, they are centrifugal. All of these 9 core families except the *Molluginaceae* and *Caryophyllaceae* have betacyanins (or in some members betaxanthins) as flower pigments, lacking anthocyanins and anthoxanthins.

The betacyanins, sometimes in the past referred to as nitrogenous anthocyanins, are a distinct chemical group of flower pigments, apparently wholly unrelated to the anthocyanins. Among closely related forms they are often replaced by the yellow betaxanthins. The structure of betaxanthins remains to be elucidated, but Mabry & Turner (40) have reasonably suggested that they may be chemically much like the betacyanins, just as the anthoxanthins are much like the anthocyanins. So far as is presently known, betacyanins and betaxanthins do no co-exist with anthocyanins or anthoxanthins in the same flower, or even in the same family; a family has one or the other type of pigment (or neither) in its flowers, but not both.

Betacyanins are presently known only from the first seven families here listed in the *Caryophyllales*, plus the *Cactaceae* and *Didiereaceae*. They have not been found in those members of the *Caryophyllaceae, Molluginaceae, Polygonaceae, Batidaceae,* and *Thelygonaceae* which have been investigated, nor have they been found in families other than those here mentioned. Mabry (41) has suggested that the *Centrospermae* be defined solely by the presence or absence of betacyanin (or betaxanthin) in the flowers, thus excluding the *Caryophyllaceae* and *Molluginaceae* and including the *Cactaceae* and *Didiereaceae*, but such a treatment would require us to ignore the rest of the evidence. One-character taxonomy, like a one-mouse experiment, is always suspect.

The close relationship of the relationship of the *Cactaceae* to the *Caryophyllales* is now well established, and this is another family which has been moved in the new Engler Syllabus. Evidence from embryology (38, 42), pollen

morphology (35), and general morphology, as well as the evidence from the chemistry of the flower pigments, supports this view. Whether the *Cactaceae* should actually be included in the *Caryophyllales* or treated as a separate but closely allied order is a matter on which opinions may legitimately differ. Buxbaum (43) has vigorously expounded the view that the *Cactaceae* should be included in the *Caryophyllales,* but I myself prefer to retain the order *Cactales.*

The affinities of the *Didiereaceae, Batidaceae,* and *Thelygonaceae* are still uncertain. Rauh and Reznik (44) believe there is hardly any room for doubt that the *Didiereaceae* must be referred to the *Centrospermae,* along with the *Cactaceae.* In addition to the pigmentation, they cite certain similarities in pollen morphology, and some successful experimental grafts of *Didiereaceae* to *Cactaceae* made by Rauh. The cross-graft might at first seem to be definitive, but surprising as it may seem, graft-compatibility bears little relation to genetic affinity. Successful cross-grafts between widely differing families have been reported, even a monocot on a dicot, although in that instance a vascular connection was not formed (45). The embryological characteristics of the *Didiereaceae* have not been fully reported, or if they have I have not found the report, but the family does differ from typical centrospermous families in lacking perisperm, the food being stored in the embryo instead. The floral morphology is also difficult to reconcile with that of the *Caryophyllales* or *Cactaceae,* being reminiscent of the *Sapindales* or the less specialized members of the *Euphorbiales* instead. Although the *Didiereaceae* may ultimately have to be included in the *Caryophyllales,* this disposition of the family should be viewed with some reserve at least until more evidence is available.

The position of the *Batidaceae* is also uncertain. In habit and inflorescence they suggest some of the *Chenopodiaceae,* but they have binucleate instead of trinucleate pollen (3), they lack perisperm as well as endosperm, and they also lack betacyanins (40). Other suggestions which have been made as to their possible relationships are also doubtful.

The *Thelygonaceae* resemble typical *Caryophyllales* in floral morphology and gross structure of the seeds, but they have only a single integument, they have endosperm instead of perisperm, and they lack betacyanins. Their affinity remains doubtful.

The *Polygonaceae* resemble the *Caryophyllales* in floral morphology, and some of them have the typical curved, peripheral embryo of the *Caryophyllales* (46) but the food storage tissue is endosperm instead of perisperm. The pollen is trinucleate, as in the *Caryophyllales* (47), and it also resembles that of some *Caryophyllales* in micromorphology. *Paronychia* and some other genera of the *Caryophyllaceae* have a reduced number of ovules (sometimes only one) and are habitally suggestive of *Polygonum.* Like the *Caryophyllaceae,* the *Polygonaceae* lack betacyanins. I personally believe the two families are fairly closely related, but not everybody agrees with me. If the *Polygonaceae* are not allied to the *Caryophyllales,* their position is uncertain.

The *Plumbaginaceae* are now generally conceded to be derived from the *Caryophyllales,* in spite of the fact that they have a straight embryo and well developed endosperm and lack betacyanins. These differences are surely as formidable

as those which have caused some botanists to question the relationship of the *Polygonaceae* to the *Caryophyllales,* but thorough study by Friedrich (48) has been generally accepted as demonstrating the ancestry of the *Plumbaginaceae* in the *Caryophyllales.* Friedrich goes so far as to include the *Plumbaginaceae* in the *Centrospermae* (*Caryophyllales*) a disposition with which most subsequent authors have not agreed, but his concepts of relationship have not been seriously challenged. All students now agree that the *Plumbaginaceae* are not closely allied to the *Primulales,* with which they have often been associated in the past.

The *Primulales* are a well defined order that seem to have their own origin among the *Polypetalae,* distinct from that of other sympetalous groups. It was at one time widely assumed that they might be derived from the *Caryophyllales,* as shown in Bessey's well known phylogenetic "cactus", but more recent opinion has tended to favor an origin in the *Guttiferales.* The free-central placentation, once seen as a strong link between the *Caryophyllales* and the *Primulales,* is now regarded as more likely a result of parallel evolution. The *Myrsinaceae,* which belong to the order *Primulales,* are tropical and woody, and presumably the ancestors of the *Primulales* as a whole should be sought among the tropical, woody groups. The *Phytolaccaceae,* of the *Caryophyllales,* do have some tropical, woody members, but these have axile rather than free-central placentation. The few other tropical, woody members of the *Caryophyllales* are too specialized in other respects to be regarded as ancestral or near-ancestral to the *Primulales.* It would therefore appear that any possible phyletic connection between the *Caryophyllales* and the *Primulales* must have antedated the development of free-central placentation in both groups. Here we have an example of the danger of postulating the ancestry of a group on the basis of the advanced members instead of the primitive ones.

The traditional *Amentiferae* consist of diverse types with reduced flowers, rather than a coherent natural group. Several of the amentiferous families, including the *Moraceae, Fagaceae, Betulaceae,* and *Casuarinaceae,* are probably related eventually to the *Rosales* through something like the *Hamamelidaceae* (49, 50).[2] Others clearly belong elsewhere. The *Garryaceae* are now generally admitted to be derived from the *Cornaceae* (51). The *Juglandaceae* and *Julianaceae* are probably related to the *Anacardiaceae,* the *Julianaceae* (52) more certainly so than the *Juglandaceae* (53). The *Salicaceae* may be allied to something in the *Violales,* such as the *Flacourtiaceae;* in any case they have nothing to do with the other amentiferous families. As we have noted, the *Batidaceae* may or may not be allied to the *Caryophyllales.*

The *Podostemaceae* and *Hydrostachyaceae,* two small families of aquatics with reduced flowers, are now usually considered to be allied to the *Rosales* (sens. lat.), and several authors, including Hutchinson, Takhtajan, and myself treat the two families as making up a single order *Podostemales.*

The *Rosales,* sens. lat., are a large and diverse group of families held together more by their evident relationship than by a set of formal characters. Here we do

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[2] Conversations with Armen Takhtajan in August, 1965 have made me receptive to the view that the *Hamamelidaceae* and their amentiferous allies may be derived directly from the Ranalian complex instead of through the *Rosales.*

approach the unfortunate condition of having an order defined by the list of families included. The diversity within the group has led some students to carve out several smaller orders, such as the *Cunoniales, Crassulales, Fabales, Hamamelidales, Pittosporales* and *Saxifragales,* but some of these are also difficult to define morphologically, and others consist only of one or a very few families. For purposes of further discussion the *Rosales* are here considered in the broad sense.

The *Rosales* are generally admitted to be derived from the Ranalian complex and to have given rise to several other groups. The *Podostemales* and some of the *Amentiferae* have already been mentioned as rosalean derivatives. The *Myrtales* are also generally conceded to be of rosalean origin, as is the large group of families that has been variously organized into the orders *Geraniales, Sapindales, Rutales, Polygalales,* and *Linales.* The number of orders to be recognized in this group, and which families to refer to which, are however still subject to considerable disagreement. The *Celastrales* and *Rhamnales* are also generally admitted to be derived from the *Rosales,* either directly or via the *Geraniales-Sapindales* complex.

The *Santalales* are generally admitted to be related to the *Celastrales,* but authors still differ as to whether they are derived directly from the *Celastrales,* or whether the two are initially parallel developments from the *Rosales.* In either case an eventual rosalean ancestry is indicated. Beginning with the *Olacaceae,* the *Santalales* show every transition from complete autotrophism through partial parasitism to complete parasitism. The nongreen family *Balanophoraceae* has traditionally been treated as a distinct order, but its relationship to the chlorophyllous members of the *Santalales* has been thoroughly demonstrated (54) and is now generally accepted.

The families *Rafflesiaceae, Hydnoraceae* and *Mitrastemonaceae,* which are intimately related among themselves, may or may not be properly referable to the *Santalales.* Traditionally they have been referred to the *Aristolochiales,* and this disposition of them has been maintained without significant comment by both Hutchinson and Takhtajan, but I find it difficult to accept. In my own opinion they are most at home in the *Santalales.*

Opinions differ as to the possible relationships of the *Umbellales* and *Cornales* to each other and to other orders, but in any case an eventual rosalean origin for both orders is indicated. In my own opinion the *Umbellales* and *Cornales* are not very closely related to each other. The *Umbellales* relate to the large group of mainly tropical trees, mostly with compound leaves, that I have referred to the order *Sapindales.* (Some of these are referred by other authors to the *Geraniales* instead). If the *Araliaceae* had the ovary superior instead of inferior, they would themselves fit nicely into this complex. The evolutionary progression from the *Araliaceae* to the *Umbelliferae* is admitted by all. The *Cornales,* on the other hand, are probably derived directly from the *Rosales.*

It is now admitted by all that the traditional *Sympetalae* are not a natural group. The probable affinities of the *Cucurbitales, Ebenales, Ericales, Primulales* and *Plumbaginales* have already been individually discussed. Once these orders have been disposed of, the rest of the *Sympetalae* pretty well hang together, so well, in fact, that it is often difficult to delimit the families. Aside from the general

morphological similarity and the transitional genera, the group is also held together by commonly having tenuinucellate ovules with a massive single integument. Unfortunately, the origin of the group is as obscure as its homogeneity is clear. The *Guttiferales*, the *Rosales*, and some things which I take to be derivatives of the *Rosales* (*Linales*, *Celastrales*, *Sapindales*) have been suggested as possible ancestors. I have not yet been able to reach an opinion on the ancestry of the group.

It has been customary to associate the *Rubiaceae* with the *Caprifoliaceae*, *Adoxaceae*, *Valerianaceae* and *Dipsacaceae* in an order *Rubiales*. There has been a current of unrest, however, in recent years about the true affinities of part or all of the *Caprifoliaceae*. *Sambucus* and *Viburnum*, in particular, are somewhat isolated within the family, and some people have speculated that one or both of them might be of a wholly different affinity. The external similarity of *Viburnum* to *Hydrangea* is obvious to anybody, but whether it reflects a real relationship is another question. I am inclined to doubt it. Now Wagenitz, in the new Engler Syllabus, has removed the *Rubiaceae* from the other families of the order (now called *Dipsacales*) and inserted the family (*Rubiaceae*) in the *Gentianales* as a near relative of the *Loganiaceae*. I have no doubt that the *Rubiaceae* are related to the *Loganiaceae*, and indeed there are two genera (*Gaertnera* and *Pagamea*) which are commonly referred to the *Rubiaceae* because of their evident relationships, but which have a superior ovary and have sometimes therefore been referred to the *Loganiaceae* instead. I do not see the need, however, to deny one relationship in affirming the other. So far as the presently available evidence is concerned, I do not see why there might not be an evolutionary line from the *Loganiaceae* through the *Rubiaceae* to the *Caprifoliaceae* and thence to the other families of the *Rubiales* (or *Dipsacales*).

The position of the *Adoxaceae* as relatives of the *Caprifoliaceae* and *Valerianaceae* has sometimes been questioned, with an affinity to the *Saxifragaceae* or some other polypetalous group being suggested instead. The traditional placement of the family receives strong support, however, from serological studies (55) which show an affinity between *Adoxa* and the *Rubiales*. The experiments showed a reaction between *Adoxa* and each of several members of the *Rubiales*, and with nothing else.

The *Callitrichaceae* are a group of aquatics with reduced, apetalous flowers. They have traditionally been referred to the *Geraniales*, where they have no obvious relatives. More recently it has become customary to associate them with the *Labiatae* and *Verbenaceae*, partly on the basis of embryological features (56). I was reluctant to take this step in my 1957 paper on the families and order of dicots, but I have been converted. This is another of the families that has been moved in the new Engler Syllabus.

I would like to be able to say that the relationships of the *Compositae* are now generally agreed upon, but unfortunately that is not so. Several years ago (57) I presented my reasons for believing them to be derived from the *Rubiales* rather than the *Campanulales*. I am still of the same opinion. Not everybody goes along with me, however, and the relationships of the *Compositae* are still controversial, even if not (in my opinion) doubtful.

Aside from the families which we are sure must be moved from their place in the traditional Englerian system, and others which can probably or surely be allowed to stay in or near their accustomed place, there are a number of families whose affinities are still controversial or uncertain. Among these, in addition to some we have already mentioned, are the *Coriariaceae, Elaeagnaceae, Euphorbiaceae, Krameriaceae, Pandaceae* and *Proteaceae.* I have an opinion on each of these, the opinion varying in strength and certitude according to the group, but some people differ with me. It remains to be seen how long it will take for a consensus to be reached.

Monocotyledons

It is universally agreed that the monocots are derived from primitive dicots, and that the monocots must therefore follow rather than precede the dicots in any proper linear sequence. The dissected stele, the herbaceous habit, the absence of intrafascicular cambium, and the monocotyledonous embryo are all seen as secondary rather than primitive characters in the angiosperms as a whole, and any plant which was more primitive than the monocots in these several respects would certainly be a dicot. The monocts are more primitive than the bulk of the dicots in mostly having monocolpate pollen (rather than tricolpate or some other type), but several of the Ranalian families also have monocolpate pollen, so there is no problem here.

For the last several decades it has been customary to think of the *Helobiae* (*Alismatales* in the broad sense) as the most primitive monocots, and to see some sort of ancestral connection from these to the dicots via such things as the *Nymphaeaceae* and *Ranunculaceae.* I think there is something in this idea, and certainly the flowers of some of the *Helobieae* are more primitive than those of other monocots in having numerous stamens and numerous spirally arranged separate pistils. The situation is more complex than appears on the surface, however. Mature seeds of the *Helobiae* uniformly lack endosperm, and in this respect they are more advanced than a great many other monocots. The *Helobiae,* or at least those members which have been examined (47), have trinucleate pollen, an advanced character shared by few other groups of monocots. If the Helobian concept of monocot evolution is to be accepted at all, we must postulate an ancestor which differed from the modern *Helobiae* in having binucleate pollen and endospermous seeds. (I continue to use the term *Helobiae* in this discussion instead of the nomenclaturally preferable *Alismatales* because the latter name has often been used in a more restricted sense.)

A more serious challenge to deriving the monocots from the vicinity of the *Nymphaeaceae* has been posed by Cheadle (58, 59), who on the basis of comparative anatomical studies sees the monocotyledonous vessel as originating wholly independently of the dicotyledonous vessel. He therefore believes that any connection between the monocots and dicots must be between the primitively vessel-less members of the groups. The *Ranunculaceae* have well developed vessels. The *Nymphaeaceae* lack vessels, but the anatomy suggests to Cheadle and others that the absence of vessels from this group is secondary rather than primitive. (However, it

may be worth noting that Takhtajan (10) considers the *Nymphaeaceae* to be primitively vessel-less.) The only vessel-less monocots so far known are aquatics—the *Lemnaceae* and certain members of the *Helobiae* (but not the *Alismataceae*). Cheadle sees nothing in any of these vessel-less monocots to suggest that any of their ancestors ever had vessels, and he feels that such an ancestry should not be lightly postulated. However, the *Lemnaceae* are on other grounds clearly to be considered as reduced derivatives from the *Araceae,* which have vessels in the roots. *Pistia,* a free-floating, aquatic, pantropical genus, is a good example of an aroid which points toward the *Lemnaceae.*

A full exposition of the matter would take more time than we have available here today, but I see no reason why the entry into an aquatic habitat by the ancestors of the present monocots might not have led to a partial or complete loss of vessels, and a cutting off of later stages in ontogeny so that only a "primitive" type of xylem was produced. To give a rough analogy, we know that the loss of a single gene can break an important biosynthetic chain in snapdragons, preventing the formation of the typical zygomorphic corolla and kicking the corolla back to the more primitive, regular form. Something similar may have happened to the xylem of the early monocots, in the absence of any selective pressure to maintain the more advanced structure. Then when descendents of these aquatic plants returned to a terrestrial habitat, a more advanced xylem structure was again developed under selective pressure.

The reason that I cling to the Helobian concept of monocot evolution is that if we abandon it, or if we deny any possible connection between the early monocots and such groups as the *Ranunculaceae* and *Nymphaeaceae,* then we create much greater obstacles to the development of a reasonable scheme than we avoid. An exploration of these problems will not be undertaken here and now; we don't have time.

An aquatic origin for the monocots provides a possible explanation for the nature of the typical monocot leaf: it is a phyllode, essentially a flattened petiole with the blade suppressed. This morphological interpretation was proposed as long ago as 1827 by deCandolle (60) and was further elaborated by Arber (61) in 1925. The transformation of a normal-looking leaf with blade and petiole to a typical monocot leaf with parallel venation can be seen under appropriate circumstances in *Sagittaria.* I was very much impressed to see all stages between the two extremes in a single population of a species of *Sagittaria* some years ago in northern Minnesota. In shallow water near the shore of the pond the leaves had normal blades and petioles. In somewhat deeper water the petiole was thinner and more flattened, and the blade was more or less reduced. In still deeper water the leaf was wholly submersed and consisted only of the flattened, thin, parallel-veined petiole, a perfectly normal monocot leaf. There was also some variation on the leaves of an individual plant, the first-formed leaves often being smaller, wholly submerged, and bladeless, whereas the later-formed ones were larger and had vestigial or more or less well developed aerial blade. This same environmentally controlled dimorphism in *Sagittaria* was reported by deCandolle.

It may well be that the leaf blade in *Sagittaria* is itself merely an expanded

petiole-tip, phylogenetically distinct from the leaf blades of dicotyledons, and that the now essentially palmate venation of some species of *Sagittaria* has been derived within the family from parallel venation, but the present structure is nonetheless that of a petiolate leaf with a well defined, palmately veined blade. It is perfectly clear that *Sagittaria* plants with the genetic potentiality to produce normal leaves can be induced to develop instead typical monocotyledonous parallel-veined leaves which are really flattened petioles. Genetic (and eventual evolutionary) fixation of a character which first appeared as a direct response to the environment is amply provided for in modern evolutionary theory (62).

Whether the interpretation that fits *Sagittaria* can be extended to the whole class *Monocotyledonae* is of course another question. I believe it can and should be so extended, and Arber gives a detailed exposition in support of this view. Under this concept terrestrial monocots with well defined, net-veined blade are considered to be derived from ancestors with narrow, parallel-veined leaves without a well defined blade, and indeed all transitional stages are seen in several families, such as the *Araceae*. An attempt to read the series the other way means that we must start with dicot-type leaves in diverse groups of monocots having nothing to do with each other, and have these all converge in both floral and vegetative characters into a hopelessly polyphyletic core of typical monocots. The resulting system, if it could be called that, would be shot full of internal contradictions.

Within the monocots, it is now clear to everybody that the *Cyperaceae, Gramineae, Sparganiaceae* and *Typhaceae* have reduced rather than primitive flowers. The *Typhaceae* and *Sparganiaceae* are closely related inter se, but they have nothing to do with the *Cyperaceae* and *Gramineae*. The relations of the order *Typhales* (including only the *Typhaceae* and *Sparganiaceae*) are obscure; perhaps they are derived eventually from something in the *Liliales*.

Among the followers of the Ranalian and Helobian school of thought it has been fairly customary to think of the *Cyperaceae* and *Gramineae* as progressively reduced types of Lilialean ancestry, with the *Juncaceae* as a sort of half-way house between the *Liliaceae* and *Cyperaceae*. This still appears to be sound at least as far as the *Cyperaceae* are concerned. In addition to the traditional characters, the discovery of the so-called diffuse centromere in both the *Cyperaceae* and *Juncaceae* (63, 64) tends to strengthen the concept that the two families are closely related. On the other hand, there is a growing current of opinion that the grasses may not be closely allied to the *Cyperaceae*. The two families are so similar in so many respects that I am reluctant to give up the thought that they are closely allied, but a mounting list of authors has felt it necessary to treat each of the two families as a monotypic order, and both Takhtajan (21) and Potzal (65) have treated the *Graminales* as being allied to the *Flagellariaceae—Restionaceae—Centrolepidaceae* cluster of families and not to the *Liliales*. On the other hand, Hutchinson (23) thinks that the *Restionaceae* and *Centrolepidaceae* are allied to the *Juncaceae*, and Koyama (66) sees the *Cyperaceae* as being allied to the *Restionaceae*, so that a relationship of the grasses to the *Restionaceae* and *Centrolepidaceae* would not be incompatable with a relationship also to the *Cyperaceae*. I want to look further into this matter before expressing an opinion.

A final point with regard to the monocots is that it is now abundantly clear that the traditional distinction between the *Liliaceae* and *Amaryllidaceae* on the basis of superior vs. inferior ovary is unnatural and must be abandoned. Inferior ovaries have been derived from superior ovaries several times in different groups of lilies. *Yucca,* with the ovary superior, is obviously related to *Agave,* with the the ovary inferior, and these and several other genera are now generally admitted to be more closely allied among themselves than any of them are to the traditional *Liliaceae* or *Amaryllidaceae.* It is now becoming customary to recognize the *Agavaceae* (including *Yucca*) as a distinct family, and to recognize several other families in the *Liliaceae-Amaryllidaceae* complex as well. The number and limits of these families are not yet agreed on, but Hutchinson's attempt to use the inflorescence instead of the position of the ovary as the critical character has not been widely accepted. This would put *Allium,* for example, in the *Amaryllidaceae* instead of in the *Liliaceae.* I would have been just as happy to expand the limits of the *Liliaceae* to include the traditional *Amaryllidaceae,* instead of trying to recognize several families, but I have sometimes been accused of being a lumper anyway.

Summary

It is now generally believed that the angiosperms were probably derived from seed ferns. This belief is based on the fact that all other groups can apparently be excluded on adequate grounds, whereas the seed ferns do have the characters from which those of the angiosperms could logically have been derived. The fossil record provides but little assistance in clarifying the ancestry of the angiosperms or their relationships inter se, but it does suggest that woody angiosperms antedate herbaceous ones; herbs do not become a prominent part of the fossil record until the beginning of the Miocene period, whereas woody groups extend back at least to the Cretaceous.

The familiar and useful Englerian system of angiosperms is now moribund, largely because it fails to recognize the significance of reduction and therefore tends to equate the simple with the primitive. With due allowance for the differences between splitters and lumpers, most of the Englerian families can stand with little or no change, but the arrangement of families into orders, and especially the concepts of relationships among the orders, must be largely recast.

Three factors combine to make the formulation of a satisfactory new system very difficult: (1) The all-pervasive parallelism within the group; (2) the seeming (or real?) lack of correlation of most of the characters marking the major groups with ecologic niches and survival value; and (3) the numerous exceptions to the characters which mark the major groups. This is about the situation one might expect if evolution at the familial and ordinal levels in angiosperms were governed largely by the supply of mutations rather than by natural selection. However, most present-day students of evolutionary theory cannot conceive of evolutionary trends or taxonomic groups that are not shaped primarily by selection, with the supply of mutations merely imposing limits on what selection can do.

No complete system which provides for all the families has yet gained general

acceptance as the successor to the Englerian system, but it is widely agreed that any acceptable new system must fall within the limits of what may be called the Ranalian concept of angiosperm evolution. Under this concept the Ranalian complex is considered to be primitive, and aggregation, fusion, reduction, and loss of parts are considered to be prominent trends in floral evolution.

Within the dicotyledons, the Ranalian complex gave rise to two major evolutionary lines (here called the Rosalean complex and the Guttiferalean complex) and several minor ones. The centrospermous complex may be a basal branch from the Guttiferalean complex, or it may be more directly derived from the Ranalian complex. The traditional *Amentiferae* consist of several different groups which have independently achieved the amentiferous condition. Most of these probably relate in one way or another to the Rosalean complex, but the *Salicales* are probably derived from the Guttiferalean complex (via the "Parietales") instead, and the *Batidales* may or may not be related to the centrospermous complex. A large proportion (but not all) of the traditional *Sympetalae* form a closely knit group whose immediate ancestry is obscure, although they must be derived eventually from the Ranalian complex.

The monocots are evidently derived from primitive dicots (i.e. from the Ranalian complex), perhaps originally as a group of aquatics more or less similar to the modern *Helobiae,* but with endospermous seeds. The typical monocot leaf with parallel venation probably represents a flattened petiole with the blade suppressed; monocots with well defined, net-veined blades probably have monocot ancestors with typical monocot leaves. The traditional distinction between the *Liliaceae* and *Amaryllidaceae* on the basis of superior or inferior ovary is unnatural and must be abandoned. Such families as the *Typhaceae, Gramineae,* and *Cyperaceae* are florally reduced rather than primitive.

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SOME NEW COMPOSITAE FROM PERU

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The 1962 Smithsonian expedition conducted by Dr. J. J. Wurdack in the region of Chachapoyas, Peru, has resulted in a great number of novelties for the Andean flora. This paper is a continuation of my contributions to the study of the *Compositae* collected in that trip. It includes descriptions of seven species belonging to *Senecio, Eupatorium, Mikania, Pappobolus* and *Vernonia* and a new genus (*Ascidiogyne*) of the *Eupatorieae.* Two new species are named in memory of the distinguished botanist and friend Robert E. Woodson. The work on which this paper is based has been sponsored by the National Science Foundation, Washington, D.C.

Senecio **woodsonianus** Cuatr., sp. nov.

Herba robusta perennis usque ad 1 m alta caulibus erectis striatis basi subteretibus 1 cm diametentibus sursum ramosis ramis striatis ad 30 cm longis foliatis et floribundis. Caules et ramuli dense glanduloso-hirtuli et albido-arachnoidei pilis patulis crassiusculis pluricellularibus basi ampliatis apice minute capitato-glandulosis copiose tecti et praecipue in juvenile pilis similibus sed apice longissime sericeo-setoso indumento aranchnoideo denso vel sparse instructis.

Folia alterna crasse herbacea rigidula sessilia oblonga apice acuta mucronulataque basi ampliata amplectentia auriculato-sagittata margine revoluta breviter dentata denticulis minutis calloso-mucronulatis, 4-7 cm longa 0.4-1.2 cm lata, nervo medio tantum conspicuo supra tenui subtus valde eminenti, utrinque dense hirto-glandulosa in juvenilia cinereo-lanuginosa vel cinereo-arachnoidea in adulta tantum subtus tomento lanuginoso supra glandulosum disposito.

Inflorescentiae paniculatae terminales plus minusve pendulae axi ramulisque striolatis flexuosis dense hirsutulo-glandulosis in sicco ferrugineis vel lutescentibus bracteis subtendentibus oblongis sessilibus sursum decrescentibus. Pedicelli flexuosi 1-2 cm longi hirto-glandulosi sursum bracteolis linearibus acutis 12-8 mm longis circa 1 mm latis instructis. Capitula discoidea campanulata 12-13 mm alta 8-10 mm lata. Involucrum circa 10 mm altum lutescenti-viride 13-15 (-21) phyllariis crasse herbaceis lanceolato-linearibus acutis extus glanduloso-hirtis pilis pluricellularibus capitulato-glandulosis ad 1 mm longis interioribus circa 10 mm longis 3-4 mm latis marginibus scariosis exterioribus 10 $\times$ 2 mm. Calyculum 5-7 bracteolis linearibus acutis 8-10 mm longis 1-1.2 mm latis ad extremum pedicelli instructis. Flores omnes hermaphroditi 45-77 in capitulo corolla lutea glabra 8-10 mm longa tubulo 3.5-4.7 mm longo limbo tubuloso dentibus triangulari-oblongis 0.8-1 mm longis acutis sursum minute papillosis. Antherae 2.5 mm longae basi auriculatae. Rami styli crassi circa 1.6 mm longi marginibus intusque stigmato-papillosi apice convexo-truncati minute papillosi penicillato-coronati extus leviter papilloso-granulati.

Ann. Missouri Bot. Gard. **52**(3): 304-313. 1965.

Achaenia oblonga 3 mm longa 10-costata costis breviter strigoso-hispidulis. Pappus 8-9 mm longus albus setis capillaribus pluriseriatis sericeis minute strigulosis. Receptaculum (4-) 5-6 (-6.5) mm diametente marginibus alveolorum breviter dentatis.

Typus: Peru, Dept Amazonas, Prov Chachapoyas: approaches to Cerro Campanario, NNE of Diosán, 3200-3500 m alt, locally frequent, flowers pale yellow, 3 Aug 1962, *J. J. Wurdack 1954.* Holotypus, US; isotypus, LIMA.

Senecio woodsonianus is closely related to *S. neoglandulosus* Cuatr. also a Peruvian species, but it differs by having discoid, larger heads, as well as larger flowers and leaves. *S. neoglandulosus* also has an arachnoid indument but only obvious on the underside of young leaves. Another related species is *S. chavanilloensis* Cuatr., which is distinguished by its radiate heads and flat, dentate leaves.

Eupatorium **ventillanum** Cuatr., sp. nov.

Suffrutex usque ad 40 cm alta caulibus teneris ramosis tortuosis saepe inferne radicantibus superne foliatis floriferisque inclinatis vel pendulis. Rami juveniles patulo-puberuli denique glaberrimi leviter striolati.

Folia opposita membranacea laete-viridia petiolata. Lamina lanceolata apicem versus attenuata acuta basi cuneata, margine inferiore parte excepto serrulata dentibus 6-8 utroque latere 2-5 cm longa 0.3-1.4 cm lata, triplinervia supra viridis costa duobusque nervis lateralibus leviter prominulis minute sparseque strigulosis reliqua glabra nervulis secundariis tenuibus vel obsoletis, subtus pallidior costa nervisque lateralibus prominulis pilosis et calloso-granulatis cetera superficie puberula pilis acutis flexuosis nervis secundariis 2 paribus ascendentibus venulis minutum discolorem reticulum formantibus. Petiolus 4-10 mm longus saepe flexuosus basi vaginato-ampliatus pilis patulis basi incrassatis copiose munitus.

Inflorescentia terminalis laxe paniculata 3-6 cm longa lataque axi ramisque teneribus hirto-pubescentibus pilis pluricellularibus acutis violaceis. Bracteolae subtendentes anguste lineares tenerae pilosae 2-4 mm longae. Pedicelli capillares 4-15 mm longi pubescentes erecti vel flexuosi 1-3 bracteolas gerentes.

Involucrum campanulatum 4-5 mm altum 2.2-3 mm diametente basi incrassato-rotundatum, phyllariis 13-15 subaequalibus subbiseriatis 3-4 mm longis 2-3 exterioribus paulo brevioribus 0.6-1.1 mm latis subscariosis linearibus acutis trinervatis margine plus minusve scariosis ciliatis dorso viridi sparsis pillis. Flores omnes hermaphroditi 20-29 in capitulum. Corolla alba 3.5-4.5 mm longa tubulo 1.5-2 longo glabro limbo subcampanulato sursum ampliato subglabro vel in lobis parcissimis pilis lobis 0.3-0.5 mm longis triangularibus intus minute papillosis. Antherae 0.8 mm longae. Rami styli 2 mm longi divaricati appendicibus albis densissime stigmato-papillosis. Achaenia nigra oblonga pentagona basi callosa angulis ciliatis. Pappus albus circa 3 mm longus setis uniseriatis strigosis. Receptaculum planum nudum glabrum minute foveolatum.

Typus: Peru, Dept Amazonas, Prov Chachapoyas: scrub forest along Río Ventilla, 1-2 km W of Molinopampa, 2350-2400 m alt, locally abundant in colonies on river banks, flowers white, 23-22 July 1962, *J. J. Wurdack 1476.* Holotypus, US; isotypus LIMA.

Eupatorium ventillanum belongs to the section *Eximbricata* (DC.) Hoffm. and is very close to the species under numbers 63-65 of Robinson's treatment of the Peruvian *Eupatoria*. The new species may be distinguished by its more slendery habit, the branches usually bending, by the more narrower, lanceolate, slender leaves with broader and more acute serrature, by the smaller size of the heads and flowers, the looser inflorescences, the longer pedicels and different kind of hairs.

Eupatorium **chachapoyasense** Cuatr., sp. nov.

Frutex 0.5-1.5 m altus ramis terminalibus foliatis densis plus minusve glandulosis spisse lanuginosis cinereis vel griseis vetustis robustis glabratis fissurato-striolatis brunnescentibus.

Folia opposita rigide crasseque coriacea petiolata. Lamina ovata vel lanceolato-ovata apice acuta basi rotundata margine basim excepto leviter revoluta breviter serrato-crenata crenaturis granulo calloso albo instructis 3-6 cm longa 1.5-3.5 cm lata, supra viridis glandulosa leviter elevato-reticulata nitidissima, subtus cinerea vel ochroleuca crasse densissimeque lanata tomento compressissimo tecta costa elevata plus minusve glabrata emergenti nervis secundariis 4-5 utroque latere patulis cum tomento velatis sed plus minusve visibilibus. Petiolus 1-2 cm longus glanduloso-resinosus lanatusque.

Inflorescentiae corymboso-paniculatae terminales folia plus minusve excedentes ramulis paucicapitatis crassiusculis glandulosis dense lanatis griseisque erectis vel subpendulis. Pedicelli 2-12 mm longi crasse spisseque lanati. Bracteae subtendentes anguste lineares 8-12 mm longae. In apice pedicellorum plerumque tantum una bracteola anguste lineari 7-8 mm longa ad involucrum adpressa instructa. Capitula crassa campanulata 9-10 mm longa circa 6 mm lata. Involucrum circa 8 mm altum glanduloso-resinosum lanatisque cinerascente, phyllariis circa 4-seriatis subaequilongis 6-7 mm longis interioribus tenuibus oblanceolatis basin versus attenuatis circa 1 mm latis subglabris, mediis exterioribusque crassiusculis rigidiusculis oblongo-lanceolatis sursum gradatim acutatis margine eroso-ciliato extus breviter sed densiuscule lanuginosis. Flores hermaphroditi 35-50 in capitulo, corolla purpurascens glabra glandulis globosis sparsis munita 4.7-5.8 mm longa tubulo circa 1.5 mm longo limbo tubuloso leviter inflato infra lobis leviter constricto dentibus oblongo-triangularibus 0.8-1 mm longis. Antherae 1.5 mm longae basi obtusae. Stylus inferne glaber ramis 3-4 mm longis linearibus obtusis papillosis. Ovarium anguste prismaticum pentagonum basim versus angustatum sparse setulosum. Pappus circa 5 mm longus setis scabrosis 1-2-seriatis robustis complanatis basi coalitis apice acutis sursum paulo dilatatis valde inaequilongis brunneo-stramineis. Receptaculum leviter convexum nudum 2-3 mm diametente.

Typus: Peru, Dept Amazonas, Prov Chachapoyas: uppermost slopes and summit of Cerros de Calla-Calla, nr kms 403-407 of Balsas Leimebamba road, 3400-3500 m alt, 18 July 1962, *J. J. Wurdack 1703.* Holotypus, US; isotypus, LIMA.

Eupatorium chachapoyasense belongs to the section *Eximbricata* having a pluriserial involucre with the phyllaries of uniform length. It is a striking species on account of its thick heads and rather robust pappus bristles, in addition to the

thick coriaceous, underneath lanate leaves. It is closely related to *E. prunifolium* H.B.K. from Ecuador, but it is readily distinguished by its larger heads with a higher number of flowers, by its more ovate leaves and by the thick, compact, lanate tomentum on the branches and under surface of the leaves.

Mikania **violaefolia** Cuatr., sp. nov.

Suffrutex scandens usque ad 2 m longa ramis volubilis tortuosis contortisque intricatis striolatis atroviolaceis glaberrimis nitidisque. Stipulae interfoliares laciniatae basi amplectentes laciniis lineari-subulatis 1-4 mm longis.

Folia opposita chartacea vere carnosula petiolata. Lamina ovato-cordata vel triangulari-cordata apice subobtusa vel subacuta breviter mucrone calloso-indurato basi profunde cordata sinu aperto vel cum lobis basalibus rotundatis vel obtuse deltoideis tegentibus margine leviter revoluta subintegra vel in juvenilis 2-3 dentibus utroque latere minutis calloso-mucronulatis in adultis granulis callosis distantibus fere obsoletis, 0.6-4 cm longa 0.5-3 cm lata, supra viridis glabra laevis plerumque tantum costa conspicua ceteris nerviis obsoletis, subtus plerumque purpurascens glabra vel subglabra minutissimis sparsissimis pilis vel granulis munita, quintuplinervia, nervis 5 crassiusculis purpuraceis glabris nervulis venulisque minutum reticulum saepe discolorem formantibus. Petiolus 0.5-2.5 cm longus purpurascens glaber basi ampliato-vaginatus amplectens.

Inflorescentiae cymoso-corymbosae terminales pedunculatae pendunculo glabro 3-6 cm longo sed aliquando longissimo (15 cm) flexuosoque tantum basi bifoliati, axi ramulisque erecti vel tortuosi striato-angulati glabri bracteolis sparsis viridibus vel violascentibus 3-8 mm longis 1.5-3 mm latis. Pedicelli 1-8 mm longi mediocres glabri vel minutissimis sparsis obsoletis pilis adpressis circa apicem bracteola lanceolato-oblonga acutata 5-6 mm longa 1.5 mm lata ad involucrum adpressa. Capitula cylindracea 8-10 mm longa circa 3 mm lata. Involucrum 8-9 mm longum, 4 phyllariis 7-8 mm longis 2.2-2.5 mm latis oblongis acutis margine hyalino-scarioso apicem versus eroso-ciliato dorso olivaceo-viridi glabro nervis obsoletis. Flores 4, corolla alba glabra circa 6 mm longa tubulo 3 mm lobis triangulari-oblongis sursum minutissime papilloso-granulatis 1.5 mm longis. Antherae atrae apice appendiculatae 1.9 mm longae. Styli dense translucide papillosi ramis 4.5-6 mm longis anguste linearibus obtusis minute stigmato-papillosis contortis. Achaenia matura 4 mm longa prysmatica 5-angulato-costata glabra. Pappus 5 mm longus albidus (pallide stramineus) setis inaequalibus pluriseriatis rigidis strigosis.

Typus: Peru, Dept Amazonas, Prov Chachapoyas: middle eastern Calla-Calla slopes, nr kms 416-419 of Leimebamba-Balsas road, 2900-3100 m alt, vine 1-2 m in shrubs, occasional, flowers white, 9 July 1962, *J. J. Wurdack 1257*. Holotypus, US; isotypus, LIMA.

Mikania violaefolia is closely related to *M. brachyphylla* Hieron., but it differs by its larger, 5-nerved leaves which are glabrous (not scabrid) above and on the main veins beneath, by the glabrous or subglabrous pedicels and involucres and by the white-stramineous pappus. The minute papillose pubescence covering the undivided part of the style is an outstanding feature of the new species.

Mikania **bulbisetifera** Cuatr., sp. nov.

Frutex scandens usque ad 2.5 mm longus ramis foliosis subteretibus striolatis ochraceo-viridibus densiuscule longe hirsuto-villosis pilis pluricellularibus acutis basi bulbosis 3-4 mm longis patulis vel flexuosis exstipulatis.

Folia opposita crasse chartacea penninervia breviter petiolata. Lamina oblongo-lanceolata basi rotundata vel obtusa apice acutissima margine leviter incurvato grosse subserrata dentibus calloso-mucronatis circa 2 mm patentibus 6-12 mm inter se distantibus, 5-10 cm longa 1.5-3.5 cm lata, supra viridis sparse pilosa granulataque tantum costa dense villosa bene conspicua ceteris nervis obsoletis subtus olivacea copiose hirto-villosa pilis longis basi bulbosis seu tuberculatis, costa prominenti denssissime villosa nervis lateralibus circa 3 utroque latere curvato-ascendentibus prominentibus nervulis reticulatis prominulis. Petiolus 5-12 mm longus crassiusculus basi dilatato-vaginatus amplectens dense hirsuto-villosus.

Inflorescentiae thyrsoideo-paniculatae terminales et axillares 15-20 cm longae, ramis patulis striolatis longe densiuscule hirsuto-setosis. Pedicelli graciles erecti setosi 2-6 mm longi. Bracteae lanceolatae acutae 4-6 mm longae 1-1.5 mm latae parce puberulae. Capitula matura 8-9 mm longa involucro 7.5 mm alto phyllariis 6.5-7 mm longis 1.5-2 mm latis oblongis sursum attenuatis acutiusculis basi incrassatis margine plus minusve hyalino-scariosis ciliatisque apice etiam ciliato ceteris glabris minute obsoleteque venoso-striolatis. Bracteola ad apicem pedicelli 4-5 mm longa 1.2-1.5 mm lata sublanceolata ad involucrum adpressa. Flores 4 hermaphroditi corolla alba 4.6-5 mm longa ad apicem dentibus parcis longis ciliis cetera glabra tubulo 1.5-1.8 mm longo lobis 1.5 mm longis oblongis margine incrassatis apice acuto minutissime papillosulo plus ciliato. Antherae 2 mm longae. Stylus glaber ramis ad 3 mm longis linearibus stigmate-papillosis contortis vel patulis. Achaenia prysmatica pentagona 3.5 mm longa glabra. Pappus 5 mm longus setis strigosis rigidis sursum leviter ampliatis.

Typus: Peru, Dept Amazonas, Prov Bongará: Jalca zone along Yambrasbamba-Pomacocha trail between Yanayacu and Pomacocha, 2300-2400 m alt, vine 1-2.5 m, in shrubs, occasional, flowers white, 26 June 1962, *J. J. Wurdack 1078.* Holotypus, US; isotypus, LIMA.

Mikania bulbisetifera is very characteristic by its abundant, villous-hirsutous indument of very long, bulbose hairs, by its oblong-lanceolate, serrate leaves and by its ciliate corolla-tips. It is closely related to *M. lasiopoda* Rob., which has entire leaves, almost glabrous above and smaller heads and flowers.

Pappobolus **woodsonianus** Cuatr., sp. nov.

Frutex circa 1 m altus ramulis terminalibus foliatis albo-lanatis et resinoso-glandulosis granulis resinosis luteis nitidis intra lanam copiosis, vetustis glabrescentibus vel glabris griseis striolatis et nodosis nodis 5-15 mm distantibus.

Folia opposita coriacea petiolata. Petiolus 6-12 mm longus supra anguste canaliculatus dense adpresseque albolanatus. Lamina ovato-oblonga basi subite angustata obtusa vel subobtusa apice attenuato-acutata margine obsolete dentata dentibus obtusissimis calloso-punctatis 1.5-5 cm longa 7-18 mm lata, supra viridis

valde strigosa subtus cinerea lana albida valde adpressa tegenti costa prominenti duobus nervis secundariis longitudinale ascendentibus notatis reliquis venulis minutum reticulum bene conspicuum formantibus.

Capitula radiata 3-4 cm diametentia (ligulis expansis) disco 1-1.5 cm diametenti 13-14 mm alto. Involucrum campanulatum basi umbilicatum 8 mm altum phyllariis circa 3-4-seriatis crasse herbaceis basi dorso calloso-incrassatis margine lanuginoso-ciliatis extus obscure nervatis vel sublaevibus subapicem glandulosis arachnoideisque vel lanuginosis reliquo subglabro, interioribus oblongis apice subite acutatis squarrosisque 7.5-8 mm longis circa 3 mm latis exterioribus similibus sed gradatim brevioribus mediis leviter ovato-oblongis ad 3.5 mm latis externis ovatis tantum ad 5 mm longis. Paleae receptaculi oblongae subite acutatae firme scariosae marginibus tenuioribus denique subcoriaceae obtusatae multivenosae plicatae dorso carinato flosculos involventes extus adpresse sericeo-puberulae 7.5-9 mm longae 4.5 mm latae.

Flores radii 10-12 ligulati neutri corolla lutea circa 14 mm longa tubulo 1-1.8 mm longo sparse pubescenti lamina oblonga conspicue 9-10-nervata apice obtusa minute tridenticulata 10-12 mm longa 3.8-5 mm lata extus praecipue in venis sericeo-pubescenti resinoso-granulataque; ovarium oblongum 3-4 mm longum sterile striatum glabrum; pappus 2-3 setis rigidulis strigosis 1.3-3 mm longis deciduis.

Flores disci hermaphroditi 28-54 corolla lutea circa 6.5 mm longa tubulo 1 mm longo limbo tubuloso sparse puberulo pilis crassiusculis brevibus copiosis dentibus triangularibus 0.8-1 mm longis incrassato-marginatis apice minutissime papillosis. Antherae 3.6 mm longae nigrae obtuse sagittatae appendice apicale ovato-laceolata. Rami styli crassiusculi lineares obtusiusculi 2 mm longi recurvati intus stigmato-papillosi extus sursum breviter papilloso-pilosi. Ovarium oblongum glabrum. Achaenium glabrum nitidum nigrum obovato-oblongum laterale subcompressum late bimarginatum parte mediali elevata (subquadrangularia) circa 3.5 mm longa 1.6 mm lata. Pappus 2-8 setis rigidis complanatis acutissimis strigosissimis valde caducis duobus marginalibus oppositis 3-4 mm longis, ceteris 1-3 mm longis aliquando deficientibus.

Typus: Peru, Dept Amazonas, Prov Chachapoyas: rocky slopes of Caño de Santa Lucía just E of Chachapoyas, 2200-2400 m alt, shrub 0.3-1 m, locally frequent, rays yellow, disc dark brown, 28 May 1962, *J. J. Wurdack 584.* Holotypus, US; isotypus, LIMA.

Pappobolus woodsonianus is a very characteristic species through its leaves which are rather small, firm, conspicuously reticulate beneath with a very compressed, cinereous, curled lanate tomentum which often makes a membranose-like surface. This thick, appressed indument distinguishes the species readily from the superficially very similar *Helianthus discolor* Bl. The kind of involucrum, paleae and especially the pappus distinguish the species from all other *Pappobolus;* it has generally up to 8 awns but they may be fewer, down to 2; these awns are narrow and strigose, like those in *Steiractinia* but here they are fewer and exceedingly deciduous. The variation in the number of awns, which, as I said before, often are

only two, and the type of achene bring this species very close to the South American *Helianthus,* but the shape of these awns makes the new species a *Pappobolus.* Blake wrote about this pappus: "The pappus awns are so extremely caducous as to render their exact enumeration very difficult"; and that is true.

This species is dedicated to the memory of the distinguished botanist and friend Robert E. Woodson.

Ascidiogyne Cuatr., gen. nov.

Capitula homogama discoidea parva. Involucrum cylindraceum phyllariis paucis plerumque 5 (4-7) biseriatis membranaceis. Receptaculum planum foveolatum nudum. Flores pauci (5-7) omnes hermaphroditi. Corolla campanulata symmetrice 5-lobata inferne in angustum tubum constricta. Antherae lobis ellipsoideo-oblongis exappendiculatis utrinque obtusis; filamenta glabra antherae aequilonga. Styli rami crassiuscule complanati oblongi apice paulo ampliato spathulato, marginibus $\frac{1}{3}$-$\frac{1}{2}$ parte inferiori dense minutissimeque stigmatico-papillosi sursum breviter denseque papillosi (marginibus dorsoque). Achaenia atro-brunnea prysmatica 5-angulata faciebus sublaevibus. Pappus squamosus translucidis calyciformibus lobato-dentatus. Membrana translucida sacciformis ovarium (vel achaenium) pappumque adherens sed separabilis involvens. Herba reptante stolonifera caespitosa. Folia opposita. Capitula axillaria pedicellata. Species typica: *Ascidiogyne wurdackii* Cuatr.

Ascidiogyne **wurdackii** Cuatr., sp. nov.—Fig. 1.

Herba prostrata reptans stolonifera intricata caule herbaceo repente valde ramoso nodoso nodis radiciferis radicibus tenuibus subcapillaribus internodiis 1-3 cm longis glabris vel sparsis pilis pluricellularibus acutis flexuosisque, terminalibus brevibus foliis congestis subfasciculatis seu subrosulatis.

Folia opposita crassiuscule herbacea viridia petiolata. Lamina obovata vel ovata apice obtusa vel rotundata vel paulo attenuata basi cuneato-angustata vel subtruncata in petiolo elongata, margine 3-5-glandulato-dentata dentibus obtusissimis vel obsoletis glandulis immersis vel paulo prominentibus, 4-10 mm longa 2.5-7 mm lata, supra glabra subtus praecipue deorsum pilis crassiusculis longis multicellularibus munita, subtrinervis costa notata subtus pilosula duobus nervis basilari-lateralibus ascendentibus conspicuis alteris venulis lateralibus ascendenti-anastomosantibus plus minusve visibilibus vel inconspicuis. Petiolus planus basi paulo ampliata circa 2 mm lata subtus margineque longe ciliatus.

Capitula homogama discoidea tubulosa axillaria solitaria pedicellata 4.5-5 mm longa. Pedicelli teretes 2-14 mm longi erecti copiose patenti-pilosi pilis articulatis acutissimis patulis usque ad 1.5 mm longis.

Involucrum tubulosum viride 4-5 mm altum 3 mm diametente phyllariis membranaceis saepe 5 quincuncialis vel 6 biseriatis, raro 7 vel 4, obovato-ellipticis apice rotundato 3.5-4 mm longis 2-1.5 mm latis interioribus valde tenuibus translucidis margine sursum eroso-ciliatis reliquum glabrum exterioribus paulo crassioribus marginibus incurvatis extus plerumque parce pilosulis.

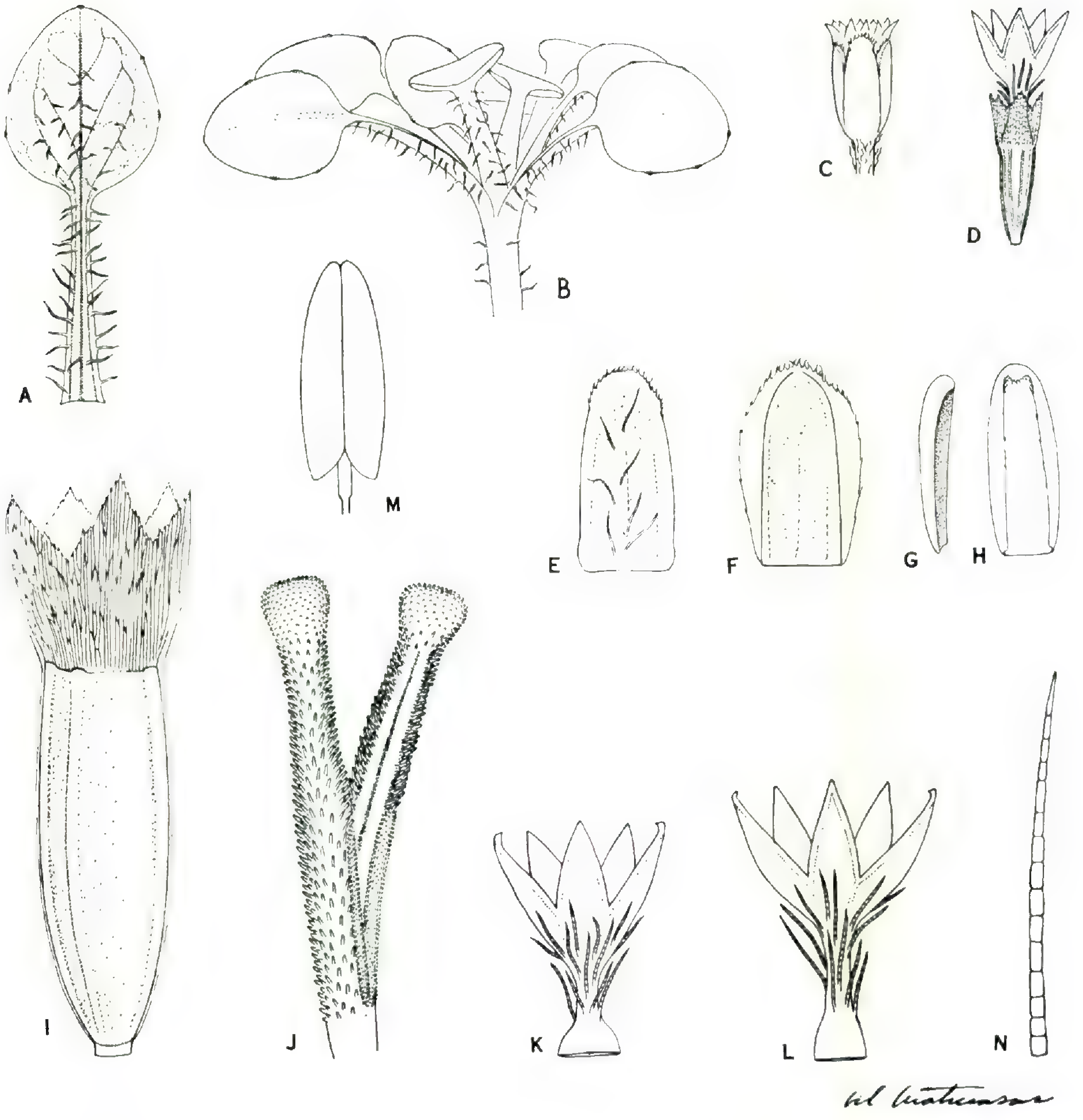

Fig. 1. *Ascidiogyne wurdackii.* A, adult leaf, underside, ×2.5; B, terminal leafy branchlet, ×2.5; C, head, ×2.5; D. flower without stamens and style, ×6; E, outer phyllary, F, inner phyllary, ×5; G, lateral view of outer phyllary; H, inner view, ×5; I, achene with pappus showing the pellicular covering membrane, ×20; J, stylar branches, ×35; K, L, corollas, ×10; M, anthers, ×30; N, hair of corolla, ×35. From *Wurdack 1716, 1246.*

Flores omnes hermaphroditi plerumque 5 vel etiam 6-7 in capitulo raro 8. Corolla alba 2-2.6 mm longa tubulo angusto basi cupulato patente-piloso 0.6-1 mm longo pilis articulatis acutis erectis 1 mm longis limbo subcampanulato profunde lobato lobis aequalibus oblongo-triangularibus acutiusculis 0.8-1 mm longis crasse marginatis glabris sed apice incurvato minutissime papilloso. Antherae atrae lobis oblongo-ellipsoideis apice obtuso exappendiculato basi obtusis 0.7-0.8 mm longae. Filamenta nuda 0.6-0.7 mm longa. Stylus erectus 2.4-2.5 mm longus trunco glaber ramis 1.2-1.3 mm longis crassis paulo complanatis marginibus incrassatis $\frac{1}{2}$-$\frac{1}{3}$ inferiori minute papilloso-stigmatiferis superne paulo angustatis marginibus dorso-

que breviter papillosis apice paulo ampliato rotundato-spathulato minute denseque papilloso; basi styli cum annulo crasso hemisphaerico cincta. Ovarium argute 5-angulatum faciebus laevibus glabris 1.6-1.7 mm longum. Pappus circa 1 mm altus membranoso-scariosus calyciformis inaequaliter 5 lobatus lobis acutis plus minusve denticulatis. Achaenia circa 0.8 mm longa prysmatica 5-angulata faciebus sublaevibus minute subgranulatis atro-brunnea. Ovaria et achaenia pappus inclusus cum vesicula pelliculoidea translucida adherenti sed separabili omnino involuta. Receptaculum planum nudum.

Typus: Peru: Dept Amazonas, Prov Chachapoyas: uppermost slopes and summit of Cerros de Calla-Calla, nr kms 403-407 of Balsas-Leimebamba road, 3400-3550 m alt, locally frequent on moist banks, flowers white, 18 Aug 1962, *J. J. Wurdack 1716.* Holotypus, US. Ibidem in open cold swamp on summit of Cerros de Calla-Calla between Leimebamba-Balsas road pass and the *camino de herradura* (2 hours walk south), 3500-3750 m occasional, corollas white, 8 July 1962, *J. J. Wurdack 1246.* Paratypus, US.

Ascidiogyne is a member of the *Eupatorieae* subtribe *Piquerinae* Hoffm. Its closest relationship is with the West Indian genus *Phania* from which it differs by its pappus with its five broad scales united in a calyx-like shape and by the smaller number of flowers and phyllaries, these being broader. But the main character of *Ascidiogyne* which distinguishes it from all other *Piquerinae* is the presence of a sack like transparent pellicle tight around the ovary and pappus, persistent on the fruit. The vesicular membrane is born on the callus at the base of the ovary and can be easily removed. The name given to the genus refers to this sack.

From the recently described Peruvian genera of *Piquerinae, Ferreyrella* and *Ellenbergia,* the new genus *Ascidiogyne,* besides its ovarium sack, differs from the first by the absence of receptacular paleae and pappus, by the actinomorphic corolla, pauciflorous heads and cespitose habit; from the second, it is well distinguished in the habit, the shape of the corolla, the style, and the pappus.

Vernonia **jalcana** Cuatr., sp. nov.

Frutex 0.5-1.5 m altus ramis densis erectis vel ascendentibus terminalibus dense foliatis striatis ochroleuco-cinereis dense adpresseque pubescenti-tomentosis.

Folia alterna petiolata coriacea rigidula. Lamina elliptico-lanceolata basi obtuse cuneata vel obtusa apice angustata subacuta vel obtusa brevissime calloso-mucronulata margine integra planaque, 2.5-5 cm longa 0.6-3 cm lata, supra luteolo-viridis scrobiculata costa dense pubescenti conspicua nervis secundariis parum visibilibus, subtus ochroleuca vel ochracea dense adpressissime pubescenti-tomentosa copiosis granulis glandulosis nitidis intra indumentum conspicuis costa elevata nervis secundariis subpatulis 7-9 utroque latere prominulis prope marginem arcuato-anastomosantibus venulis minoribus saepe inconspicuis. Petiolus crassus 4-5 mm longus dense pubescens supra planus basi incrassatus.

Inflorescentiae subcorymboso-paniculatae rotundatae terminales folia suprema excedentes ramis ramulisque ascendentibus argute angulatis ancipitatis dense adpresseque tomentoso-pubescentibus ebracteatis, capitulis densis saepe glomeratis

3-5 in extremo ramusculorum sessilibus vel subsessilibus pedicellis usque ad 1 mm longis vel pseudo-pedicellis (ramulis unicapitatis) ad 5 mm longis. Capitula tubulosa 8-10 mm longa circa 2.5 mm lata. Involucrum tomentellum 6.5-7.5 mm longum phyllariis 5-6-seriatis subscariosis apicem versus glanduloso-granulatis extus dense pubescentibus interioribus oblongo-lanceolatis 5-6 mm longis 1.2-1.5 mm latis apice acutatis, mediis oblongo-ovatis acutis ad 2 mm latis, exterioribus basalibus ovatis subite acutatis vel obtusatis 2-1 mm longis latisque. Flores 3 in capitulo, corolla purpurascenti vel lilacina circa 8 mm longa tubuloso infundibuliformi sparse glanduloso-granulata tubulo circa 1.5 mm longo lobis linearibus acutatis incrassato-marginatis extremo extus dense glanduloso-granulatis. Antherae 3 mm longae sagittatae caudicibus obtusiusculis coalitis. Filamenta glabra. Stylus ramis lineari-subulatis 2-2.5 mm longis extus hispidulis parte integra sursum (1 mm longitudine) hispidulus ceteris glaber. Ovarium 1.5-2 mm longum oblongum argute 10-costato-sulcatum in sulcis glanduloso-granulatum basi crasse callosum. Pappus albus 5.5-7 mm longus setis basi coalitis interioribus capillaribus minute strigulosis exterioribus brevibus tenuioribus acutis circa 1 mm longis (0.5-2 mm). Receptaculum breve (0.7-0.8 mm diam) convexum nudum.

Typus: Peru, Dept Amazonas, Prov Chachapoyas: Jalca zone 1-5 km W of Molinopampa 2400-2450 m alt, shrub 0.5-1.5 m, frequent, heads lilac, 18 July 1962, *J. J. Wurdack 1359;* Holotypus, US; isotypus, LIMA. Prov Bongará: Jalca zone 3 km S of Pomacocha, E of Shipasbamba trail, 2400 m, shrub 0.5-1.5 m, frequent, flowers purple, 20 June 1962, *J. J. Wurdack 971.* Paratypi, US, LIMA.

Vernonia jalcana is an outstanding species of the section *Critoniopsis* well distinguished by its rather small, coriaceous leaves which are glabrous and scrobiculate above and densely villous-tomentose beneath, by its almost corymbose panicles, by its pubescent involucres and by other details of the flowers.

KEYS FOR THE IDENTIFICATION OF SEEDLINGS OF SOME PROMINENT WOODY SPECIES IN EIGHT FOREST TYPES IN PUERTO RICO[1, 2, 3]

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In 1963 and 1964, I studied seedlings in preparation for successional investigations in Puerto Rico. Most seedlings were observed in the field, but some were raised from seed at Beltsville. I have constructed keys for the woody seedlings observed in the following forest types: (1) mangrove woodlands, (2) littoral woodlands, (3) dry limestone forests, (4) dry coastal forests, (5) moist coastal and limestone forests, (6) lower cordillera and lower Luquillo forests, (7) upper cordillera and upper Luquillo forests, and (8) gardens and parks. The choice of these forest types results from my observations and those of Little & Wadsworth (Common trees of Puerto Rico and the Virgin Islands. Agr. Handb. No. 249. USDA For. Serv. 548 p. 1964). I have assigned each species to the forest type in which I think it is most likely to occur. In Appendix 1, botanical and Spanish names of the species are accompanied by references to the illustrations and to the forest type or types in which the seedlings occur.

In the lower cordillera and lower Luquillo forests, most seeds germinate in or on the litter above the soil. In nearly half of these, the cotyledons do not emerge from the testa during germination. It is etymologically incorrect to term such germination hypogeal. Therefore, I propose the following adjectives: (1) *cryptocotylar* (*crypto,* hidden; *cotyledon,* a hollow vessel), characterized by the cotyledons remaining in the testa after germination; and (2) *phanerocotylar* (*phanero,* manifest; *cotyledon,* a hollow vessel), characterized by the cotyledons escaping the testa during germination. There is a gradual increase in the percentage of cryptocotylar species as one passes from the dry limestone forests (thorn forests) to the lower cordillera and lower Luquillo forests (rain forests).

Three more words have facilitated the construction of the keys: (1) *cataphylls*: brown or hyaline scale leaves succeeding the cotyledons, as in many cryptocotylar species, (2) *eophylls*: the first few leaves with green expanded laminae (Tomlinson, J. Arnold Arb. **41:** 415. 1960), and (3) *metaphylls*: the mature leaves as opposed to the juvenile forms (Jackson's glossary).

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[1] This research is sponsored by the Advanced Research Projects Agency, Department of Defense.

[2] Illustrations, by Peggy K. Duke, were prepared as part of the Rain Forest Project of the Puerto Rico Nuclear Center at El Verde, Puerto Rico, supported by the Division of Biology and Medicine of the Atomic Energy Commission.

[3] Cost of reproducing plates was subsidized by the Puerto Rico Nuclear Center.

KEY 1. MANGROVE WOODLANDS

A. Seedlings cryptocotylar.
  B. Eophylls opposite; vernation convolute ....(Fig. 142) RHIZOPHORA MANGLE
  BB. Eophylls alternate; vernation not convolute.
    C. Eophylls imparipinnate; cataphylls prominent ....(Fig. 58) MACHAERIUM LUNATUM
    CC. Eophylls simple; cataphylls inconspicuous or absent ....(Fig. 54) PTEROCARPUS OFFICINALIS
AA. Seedlings phanerocotylar.
  D. Cotyledons conduplicate ....(Fig. 166) AVICENNIA GERMINANS
  DD. Cotyledons not conduplicate.
    E. Cotyledons convolute; leaves often basally biglandular.
      F. Leaves opposite ....(Fig. 136) LAGUNCULARIA RACEMOSA
      FF. Leaves alternate ....(Fig. 133) CONOCARPUS ERECTUS
    EE. Cotyledons not convolute; leaves not basally biglandular.
      G. Leaves stipulate; latex absent.
        H. Cotyledons more than 15 mm long, much broader than long ....(Fig. 116) THESPESIA POPULNEA
        HH. Cotyledons less than 15 mm long, scarcely broader than long ....(Fig. 114) HIBISCUS TILIACEUS
      GG. Leaves exstipulate; latex present.
        I. Leaves opposite ....(Fig. 127) CLUSIA sp.
        II. Leaves alternate ....(Fig. 149) MANILKARA BALATA

KEY 2. LITTORAL WOODLANDS

A. Seedlings cryptocotylar.
  B. Venation parallel ....(Fig. 5) COCOS NUCIFERA
  BB. Venation not parallel.
    C. Seedlings unarmed ....(Fig. 35) CHRYSOBALANUS ICACO
    CC. Seedlings armed ....(Fig. 20) XIMENIA AMERICANA
AA. Seedlings phanerocotylar.
  D. Cotyledons bilobate ....(Fig. 152) IPOMOEA PES-CAPRAE
  DD. Cotyledons entire or retuse.
    E. Cotyledons as broad as long or broader, often retuse.
      F. Leaves ocreate ....(Fig. 18) COCCOLOBA UVIFERA
      FF. Leaves not ocreate.
        G. Cotyledons retuse, not convolute; eophylls dentate ....(Fig. 172) TECOMA STANS
        GG. Cotyledons entire, convolute; eophylls entire ....(Fig. 134) TERMINALIA CATAPPA
    EE. Cotyledons longer than broad, entire.
      H. Cotyledons linear; eophylls dentate ....(Fig. 104) DODONAEA VISCOSA
      HH. Cotyledons lanceolate to ovate; eophylls entire.
        I. Cotyledons convolute; leaves lepidote ....(Fig. 26) CAPPARIS CYNOPHALLOPHORA

II. Cotyledons not convolute; leaves elepidote.
J. Latex present; leaves opposite........(Fig. 157) CALOTROPIS PROCERA
JJ. Latex absent; leaves verticillate ..(Fig. 7) CASUARINA EQUISETIFOLIA

KEY 3. DRY LIMESTONE FORESTS (THORN FORESTS)

A. Seedlings cryptocotylar.
B. Eophylls compound.
C. Eophylls decompound ....(Fig. 29) MORINGA OLEIFERA
CC. Eophylls not decompound.
D. Eophylls trifoliolate ....(Fig. 100) SERJANIA POLYPHYLLA
DD. Eophylls bifoliolate or quadrifoliolate ....(Fig. 37) PITHECELLOBIUM UNGUIS-CATI
BB. Eophylls simple ....(Fig. 103) THOUINIA PORTORICENSIS

AA. Seedlings phanerocotylar.
E. Latex present ....(Fig. 158) PLUMERIA ALBA
EE. Latex absent.
F. Cotyledons deeply retuse or bilobate.
G. Eophylls simple.
H. Cotyledons about as broad as long, shallowly retuse ....(Fig. 170) CRESCENTIA CUJETE
HH. Cotyledons much broader than long, deeply retuse ....(Fig. 167) TABEBUIA HETEROPHYLLA
GG. Eophylls paripinnate ....(Fig. 49) HAEMATOXYLON CAMPECHIANUM
FF. Cotyledons entire or rarely shallowly emarginate.
I. First or second eophylls compound or lobed.
J. Eophylls with fewer than six leaflets or lobes.
K. Eophylls palmately lobed ....(Fig. 79) JATROPHA GOSSYPIFOLIA
KK. Eophylls pinnate ....(Fig. 57) PICTETIA ACULEATA
JJ. Eophylls with more than five leaflets.
L. First two eophylls at the cotyledonary node, pinnate.
M. Cotyledons trinerved ....(Fig. 51) PARKINSONIA ACULEATA
MM. Cotyledons uninerved ....(Fig. 40) ACACIA FARNESIANA
LL. First two eophylls above the cotyledonary node, pinnate or 2-pinnate.
N. First two eophylls opposite; cotyledons plano-convex ....(Fig. 52) TAMARINDUS INDICA
NN. First two eophylls alternate; cotyledons not plano-convex.
O. Leaflets 2-4 mm long ......(Fig. 41) PROSOPIS JULIFLORA
OO. Leaflets 6-10 mm long ....(Fig. 42) LEUCAENA LEUCOCEPHALA
II. First and second eophylls simple.
P. Cotyledons or eophylls convolute.
Q. Cotyledons convolute; eophylls strict ....(Fig. 27) CAPPARIS COCCOLOBIFOLIA
QQ. Cotyledons not convolute; eophylls convolute ....(Fig. 62) ERYTHROXYLON AREOLATUM

PP. Cotyledons and eophylls not convolute.
R. Eophylls alternate.
S. Eophylls subsessile, ocreate, entire ....(cf. Fig. 16) COCCOLOBA sp.
SS. Eophylls petiolate, not ocreate, entire to lobate.
T. Seedlings pilose with long hairs..(Fig. 83) CROTON LUCIDA
TT. Seedlings without long hairs.
U. Cotyledons broadly reniform; metaphylls lobed ....(Fig. 112) GOSSYPIUM ARBOREUM
UU. Cotyledons ovate; metaphylls compound ....(Fig. 65) AMYRIS ELEMIFERA
RR. Eophylls opposite.
V. Cotyledons foliaceous, green.
W. Seeds alate; stipules amplexicaul ....(Fig. 179) EXOSTEMA CARIBAEUM
WW. Seeds exalate; stipules filiform ....(Fig. 109) COLUBRINA ARBORESCENS
VV. Cotyledons planoconvex, brown ....(Fig. 89) SAVIA SESSILIFLORA

KEY 4. DRY COASTAL FORESTS (DECIDUOUS SEASONAL FORESTS)

A. Seedlings cryptocotylar.
B. Venation parallel ....(Fig. 2) SABAL CAUSIARUM
BB. Venation not parallel.
C. Eophylls simple.
D. Eophylls entire, alternate.
E. Seeds alate; leaves acuminate, drooping, without a white border ....(Fig. 73) SWIETENIA MAHAGONI
EE. Seeds exalate; leaves not acuminate or drooping, with a white border ....(Fig. 150) BUMELIA OBOVATA
DD. Eophylls dentate or undulate, the first pair usually opposite ....(cf. Fig. 75) TRICHILIA HIRTA
CC. Eophylls bifoliolate ....(Fig. 107) MELIOCOCCUS BIJUGATUS

AA. Seedlings phanerocotylar.
F. Cotyledons plicate, dentate.
G. Veins orange ....BOURRERIA SUCCULENTA
GG. Veins green ....(Fig. 159) CORDIA NITIDA
FF. Cotyledons not plicate or dentate.
H. Cotyledons trifoliolate ....(Fig. 69) BURSERA SIMARUBA
HH. Cotyledons simple.
I. Eophylls compound.
J. Eophylls trifoliolate or palmate ....(Fig. 118) CEIBA PENTANDRA
JJ. Eophylls pinnate.
K. Eophylls with 4-6 leaflets; seeds brownish-orange.
L. Metaphylls mostly 4-foliolate ....(cf. Fig. 70) GUAIACUM OFFICINALE
LL. Metaphylls mostly 6-10-foliolate ....(Fig. 70) GUAIACUM SANCTUM
KK. Eophylls with more than 6 leaflets; seeds bright red ....(Fig. 39) ADENANTHERA PAVONINA

II. Eophylls simple.
M. Cotyledons broader than long.
N. Eophylls dentate; cotyledons retuse ....(Fig. 169) SPATHODEA CAMPANULATA
NN. Eophylls entire; cotyledons mucronate ....(Fig. 135) BUCIDA BUCERA
MM. Cotyledons longer than broad.
O. Cotyledons planoconvex ....(Fig. 90) ANACARDIUM OCCIDENTALE
OO. Cotyledons flat.
P. Latex present ....(Fig. 11) FICUS CITRIFOLIA
PP. Latex absent.
Q. Eophylls dentate.
R. Eophylls cordate, more than 3 cm long ....(Fig. 86) HURA CREPITANS
RR. Eophylls not cordate, less than 3 cm long ......(Fig. 165) CITHAREXYLUM FRUTICOSUM
QQ. Eophylls entire.
S. Cotyledons longer than 1.5 cm ....(Fig. 96) CASSINE XYLOCARPA
SS. Cotyledons shorter than 1.5 cm ....(Fig. 95) SCHAEFFERIA FRUTESCENS

Key 5. MOIST COASTAL AND LIMESTONE FORESTS (SEMI-EVERGREEN SEASONAL FORESTS)

A. Seedlings cryptocotylar.
B. Venation parallel; seedling armed ....(Fig. 6) ACROCOMIA MEDIA
BB. Venation not parallel; seedling unarmed.
C. Cataphylls opposite or subopposite; latex yellow ....(Fig. 125) CALOPHYLLUM CALABA
CC. Cataphylls alternate or absent; latex, if present, watery or milky.
D. Eophylls peltate ....(Fig. 21) HERNANDIA SONORA
DD. Eophylls not peltate.
E. Eophylls pinnate or palmately lobed.
F. Eophylls pinnate ....(Fig. 55) ANDIRA INERMIS
FF. Eophylls palmately lobed ....(Fig. 123) STERCULIA APETALA
EE. Eophylls simple.
G. Seeds subglobose; cotyledons not obviously dissimilar.
H. Eophylls obviously penninerved; seeds usually more than 2 cm broad, brown, dull ....(Fig. 23) PERSEA AMERICANA
HH. Eophylls uninerved or weakly penninerved; seeds less than 2 cm broad, black, lustrous ....(Fig. 99) SAPINDUS SAPONARIA
GG. Seeds ovoid; cotyledons markedly dissimilar ....(Fig. 12) ARTOCARPUS HETEROPHYLLUS
AA. Seedlings phanerocotylar.
I. First eophylls stipulate, opposite, simple.
J. Metaphylls simple.
K. Leaves glabrous, vernicose ....(Fig. 177) TEREBRARIA RESINOSA
KK. Leaves hairy, not vernicose ....(Fig. 176) GUETTARDA sp.

JJ. Metaphylls bifoliolate ....(Fig. 48) HYMENAEA COURBARIL

II. First eophylls, if stipulate, not opposite and simple.

L. Eophylls trifoliolate.

M. Cotyledons lance-oblong; eophylls punctate (Fig. 66) ZANTHOXYLUM sp.

MM. Cotyledons linear; eophylls not punctate ....(Fig. 93) SPONDIAS PURPUREA

LL. Eophylls simple.

N. Latex present ....(Fig. 84) SAPIUM LAUROCERASUS

NN. Latex absent.

O. Cotyledons plicate, dentate.

P. Seedling cepaceous ....CORDIA ALLIODORA

PP. Seedling not cepaceous ....(Fig. 160) CORDIA SULCATA

OO. Cotyledons not plicate nor dentate.

Q. Cotyledons punctate.

R. Cotyledons acute, lanceolate ..(Fig. 137) PSIDIUM GUAJAVA

RR. Cotyledons obtuse, ovate to reniform.

S. Cotyledons contortuplicate, nigrid-punctate ....(Fig. 115) MONTEZUMA SPECIOSISSIMA

SS. Cotyledons plane, red-punctate ....(Fig. 162) TECTONA GRANDIS

QQ. Cotyledons not punctate.

T. Cotyledons subsessile.

U. Teeth of the eophylls longer than broad or ciliate; indument of the lower surface not arachnoid.

V. Eophylls subglabrous, usually with fewer than 14 teeth ....(Fig. 148) DENDROPANAX ARBOREUS

VV. Eophylls pilose, usually with more than 14 teeth ....(Fig. 144) DIDYMOPANAX MOROTOTONI

UU. Teeth of the eophylls nearly as broad as long; indument of the lower surface arachnoid.

W. Petiolar indument ferrugineous; hypocotyl densely pubescent ....(Fig. 119) OCHROMA PYRAMIDALE

WW. Petiolar indument not ferrugineous; hypocotyl scantily pubescent ....(Fig. 13) CECROPIA PELTATA

TT. Cotyledons long-petiolate.

X. Eophylls dentate, pilose ..(Fig. 111) TRIUMFETTA sp.

XX. Eophylls entire, glabrous or subglabrous ....(Fig. 164) CESTRUM MACROPHYLLUM

KEY 6. LOWER CORDILLERA AND LOWER LUQUILLO FORESTS (RAIN FORESTS)

A. Seedlings cryptocotylar.

B. Eophylls compound.

C. Eophylls bifoliolate.

D. Petiole strongly alate, with a gland at the summit ....(Fig. 34) INGA VERA

DD. Petiole weakly alate or exalate, glandless ....(Fig. 32) INGA FAGIFOLIA

CC. Eophylls trifoliolate or pinnate.

E. Eophylls with many leaflets ....(Fig. 33) PITHECELLOBIUM ARBOREUM

EE. Eophylls with usually three leaflets.

F. First eophylls alternate, the leaflets dentate ....(Fig. 91) COMOCLADIA GLABRA

FF. First eophylls opposite, the leaflets entire....(Fig. 71) DACRYODES EXCELSA

BB. Eophylls simple.

G. Eophylls entire.

H. Latex absent.

I. Eophylls, at least after the first pair, alternate.

J. Venation parallel or plinerved.

K. Venation parallel ....(Fig. 3) ROYSTONEA BORINQUENA

KK. Venation plinerved ....(Fig. 8) SMILAX cf. CORIACEA

JJ. Venation not parallel or plinerved.

L. Petioles incrassate.

M. Seed red, subglobose ....(Fig. 56) ORMOSIA KRUGII

MM. Seed brown, reniform.

N. Eophylls stipulate ....(Fig. 61) ERYTHRINA cf. POEPPIGIANA

NN. Eophylls exstipulate ....((Fig. 31) ROUREA SURINAMENSIS

LL. Petioles not incrassate.

O. Seeds flattened and often winged.

P. Seeds winged; embryo less than 1.5 cm long.

Q. Eophylls all alternate, less than 2 cm long ....(Fig. 78) SECURIDACA DIVERSIFOLIA

QQ. First eophylls opposite, more than 2 cm long ....(Fig. 72) SWIETENIA MACROPHYLLA

PP. Seeds not winged; embryo more than 1.5 cm long ....(Fig. 94) MANGIFERA INDICA

OO. Seeds globose to ovoid.

R. Stipules obvious.

S. First eophylls alternate, densely pubescent ....(Fig. 36) HIRTELLA RUGOSA

SS. First eophylls opposite, glabrous ....(Fig. 117) QUARARIBEA TURBINATA

RR. Stipules not obvious.

T. Hypocotyl conspicuously pubescent; seeds less than 2.5 cm long.

U. Leaves yellowish-green, wartless ....(Fig. 22) NECTANDRA ANTILLANA

UU. Leaves green, often with conical warts ....(Fig. 24) OCOTEA LEUCOXYLON

TT. Hypocotyl subglabrous; seeds more than 2.5 cm long ..(Fig. 25) OCOTEA MOSCHATA

II. Eophylls opposite.

V. Seeds subglobose, exalate.

W. Seedling aromatic, not fuliginous ....(Fig. 141) EUGENIA STAHLII

WW. Seedling not aromatic, often fuliginous ....(Fig. 143) EUGENIA JAMBOS

VV. Seeds flattened, alate ....(Fig. 67) HETEROPTERIS LAURIFOLIA

HH. Latex present.
- X. Leaves opposite .... (Fig. 124) RHEEDIA PORTORICENSIS
- XX. Leaves alternate .... (Fig. 153) POUTERIA MULTIFLORA

GG. Eophylls dentate or undulate.
- Y. Teeth of eophylls acute; seeds brown to black.
  - Z. Seeds exalate; third eophyll simple.
    - a. First eophylls less than 2 cm long; metaphylls unifoliolate .... (Fig. 101) ALLOPHYLUS CRASSINERVIS
    - aa. First eophylls more than 2 cm long; metaphylls compound .... (Fig. 102) CUPANIA AMERICANA
  - ZZ. Seeds alate; third eophyll trifoliolate .. (Fig. 105) PAULLINIA PINNATA
- YY. Teeth of eophylls rounded; seeds reddish.
  - b. Eophylls mostly less than 3 cm long ...... (Fig. 75) TRICHILIA PALLIDA
  - bb. Eophylls mostly more than 3 cm long.
    - c. Metaphylls 8-20-foliolate, the tertiary veins obscure above .... (Fig. 74) GUAREA GUIDONIA
    - cc. Metaphylls 2-6-foliolate, the tertiary veins prominent on both sides .... (Fig. 77) GUAREA RAMIFLORA

AA. Seedlings phanerocotylar.
- d. Eophylls not entire; metaphylls alternate.
  - e. Leaves lobed; yellow latex present. .... (Fig. 28) BOCCONIA FRUTESCENS
  - ee. Leaves dentate, serrate, or denticulate; yellow latex absent.
    - f. Leaves exstipulate.
      - g. Cotyledons plicate, dentate.
        - h. Leaves scabrous .... (Fig. 161) CORDIA LIMA
        - hh. Leaves not scabrous. .... (Fig. 163) CORDIA BORINQUENSIS
      - gg. Cotyledons not plicate or dentate.
        - i. Eophylls less than 3 cm long.
          - j. Leaves pubescent.
            - k. Leaves oblanceolate, short-petiolate. .... (Fig. 146) RAPANEA FERRUGINEA
            - kk. Leaves ovate, long-petiolate. .... (Fig. 85) ALCHORNEOPSIS PORTORICENSIS
          - jj. Leaves glabrous .... (Fig. 92) ILEX NITIDA
        - ii. Eophylls more than 3 cm long .... (Fig. 108) MELIOSMA HERBERTII
    - ff. Leaves stipulate.
      - l. Petioles incrassate; eophylls more than 2.5 cm long .... (Fig. 113) SLOANEA BERTERIANA
      - ll. Petioles not incrassate; eophylls less than 2.5 cm long.
        - m. Cotyledons reniform, with petioles about as long as the blades .... (Fig. 14) URERA BACCIFERA
        - mm. Cotyledons, if reniform, with petioles shorter than the blades.
          - n. Teeth of eophylls remote, usually fewer than 12 .... (Fig. 129) HOMALIUM RACEMOSUM
          - nn. Teeth of eophylls approximate, usually more than 12.
            - o. Leaves broader above the middle, oblanceolate .... (Fig. 131) CASEARIA ARBOREA
            - oo. Leaves broader below the middle, ovate.
              - p. First eophylls opposite, serrate .... (Fig. 128) CASEARIA GUIANENSIS
              - pp. First eophylls alternate, dentate .... (Fig. 130) CASEARIA SYLVESTRIS

dd. Eophylls entire; metaphylls alternate or opposite.

q. Seedling laticiferous.

r. Second pair of leaves opposite; metaphylls stipulate ....(cf. Fig. 11) FICUS spp.

rr. Leaves after the first pair alternate; metaphylls exstipulate ....(Fig. 156) PLUMERIA OBTUSA

qq. Seedlings not laticiferous.

s. Metaphylls opposite.

t. Cotyledons stipulate.

u. Cotyledons as broad as long or broader, short-petiolate.

v. Cotyledons reniform ....(Fig. 182) COFFEA ARABICA

vv. Cotyledons broadly deltoid.

w. Cotyledons about as broad as long; stipules lanceolate ....(Fig. 180) GENIPA AMERICANA

ww. Cotyledons broader than long; stipules linear ....(Fig. 181) IXORA FERREA

uu. Cotyledons longer than broad, long-petiolate.

x. Seedlings densely pubescent ....(Fig. 176) GUETTARDA sp.

xx. Seedlings not densely pubescent.

y. Leaf blades decurrent ....(Fig. 178) PALICOUREA ALPINA

yy. Leaf blades not decurrent ..(cf. Fig. 174) PSYCHOTRIA spp.

tt. Cotyledons not stipulate.

z. Leaves plinerved .... MICONIA spp.

zz. Leaves not plinerved.

A. Cotyledons about as long as broad.

B. Second pair of eophylls broader above the middle; lateral veins few, remote ....(Fig. 138) GOMIDESIA LINDENIANA

BB. Second pair of eophylls broader below the middle; lateral veins numerous, approximate ....(Fig. 140) MYRCIA SPLENDENS

AA. Cotyledons much longer than broad.

C. Cotyledons ovate ......(Fig. 154) LINOCIERA DOMINGENSIS

CC. Cotyledons lanceolate ....(Fig. 63) BYRSONIMA CORIACEA

ss. Metaphylls alternate.

D. Cotyledons plano-convex; metaphylls compound ....(Fig. 68) TETRAGASTRIS BALSAMIFERA

DD. Cotyledons foliaceous; metaphylls simple.

E. Nodes ocreate or geniculate.

F. Veins strongly ascending.

G. Upper leaf surface with conspicuous septate hairs; margin not ciliate ..(Fig. 9) PIPER TRELEASEANUM

GG. Upper leaf surface without conspicuous septate hairs; margin short-ciliate ....(Fig. 10) PIPER ADUNCUM

FF. Veins not strongly ascending ....(cf. Fig. 16) COCCOLOBA sp.

EE. Nodes not ocreate or geniculate.

H. Cotyledons linear ....(Fig. 17) CISSAMPELOS PAREIRA

HH. Cotyledons broader than linear.

I. Seedlings aromatic ....(Fig. 15) GUATTERIA CARIBAEA

II. Seedlings not aromatic.

J. Petioles incrassate ....(Fig. 113) SLOANEA BERTERIANA

JJ. Petioles not incrassate.
K. Cotyledons reniform.
............................(Fig. 139) BUCHENAVIA CAPITATA
KK. Cotyledons ovate.
L. Leaves punctate
......................(Fig. 147) ARDISIA GLAUCIFLORA
LL. Leaves not punctate
................................(Fig. 87) DRYPETES GLAUCA

KEY 7. UPPER CORDILLERA AND UPPER LUQUILLO FORESTS (MOSSY FORESTS)

A. Seedlings cryptocotylar.
B. Eophylls bilobed or compound; seedlings not aromatic.
C. Venation parallel ....(Fig. 4) PRESTOEA MONTANA
CC. Venation pinnate ....(Fig. 106) MATAYBA DOMINGENSIS
BB. Eophylls simple; seedlings aromatic.
D. Leaves alternate ....(Fig. 30) OCOTEA SPATHULATA
DD. Leaves opposite ....(Fig. 145) EUGENIA BORINQUENSIS

AA. Seedlings phanerocotylar.
E. Cotyledons stipulate; metaphylls opposite.
F. Seedlings malodorous.
G. Stipules connate ....PSYCHOTRIA MALEOLENS
GG. Stipules free ....LASIANTHUS LANCEOLATUS
FF. Seedlings not malodorous ....(Fig. 173) HILLIA PARASITICA
EE. Cotyledons not stipulate; metaphylls alternate or opposite.
H. Cotyledons linear.
I. Cotyledons with two nerves ....(Fig. 1) PODOCARPUS CORIACEUS
II. Cotyledons with one or three nerves ....(Fig. 98) CYRILLA RACEMIFLORA
HH. Cotyledons not linear.
J. Eophylls trifoliolate ....(Fig. 97) TURPINIA PANICULATA
JJ. Eophylls simple.
K. Eophylls dentate ....(Fig. 82) ALCHORNEA LATIFOLIA
KK. Eophylls entire.
L. Latex present.
M. Latex white.
N. Petioles and midribs with many appressed hairs; metaphylls apiculate
............(cf. Fig. 151) MICROPHOLIS CHRYSOPHYLLOIDES
NN. Petioles and midribs with few scattered hairs; metaphylls not apiculate
.........................(Fig. 151) MICROPHOLIS GARCINIAEFOLIA
MM. Latex yellow ....(Fig. 127) CLUSIA sp.
LL. Latex absent.
O. Leaves alternate.
P. Cotyledons broader than long, retuse
....(Fig. 168) TABEBUIA RIGIDA
PP. Cotyledons longer than broad, not retuse
....(Fig. 88) CROTON POECILANTHUS
OO. Leaves opposite.
Q. Leaves plinerved.
R. Leaves obtuse, lepidote
..................................CALYCOGONIUM SQUAMULOSUM

RR. Leaves acute, stellate-pubescent .... HETEROTRICHUM CYMOSUM
QQ. Leaves penninerved.
S. Nodes incrassate .... (Fig. 132) DAPHNOPSIS PHILIPPIANA
SS. Nodes not incrassate (Fig. 155) HAENIANTHUS SALICIFOLIUS var. OBOVATUS

KEY 8. GARDENS AND PARKS

A. Seedlings cryptocotylar.
B. Eophylls pellucid-punctate .... CITRUS sp.
BB. Eophylls not pellucid-punctate.
C. Latex present.
D. Eophylls trifoliolate .... (Fig. 76) HEVEA BRASILIENSE
DD. Eophylls simple .... (Fig. 126) GARCINIA MANGOSTANA
CC. Latex absent.
E. First eophylls simple.
F. Eophylls exstipulate .... (Fig. 19) ANNONA SQUAMOSA
FF. Eophylls stipulate .... (Fig. 60) ERYTHRINA CRISTA-GALLI
EE. First eophylls compound.
G. Eophylls quadrifoliolate .... (cf. Fig. 37) PITHECELLOBIUM DULCE
GG. Eophylls palmate .... PACHIRA AQUATICA

AA. Seedlings phanerocotylar.
H. First eophylls compound or palmately lobed.
I. Cotyledons linear; eophylls decompound .... MELIA AZEDERACH
II. Cotyledons broader than linear; eophylls lobed to decompound.
J. Eophylls palmately compound or lobed.
K. Cotyledons convolute; eophylls 5-foliolate .... (Fig. 122) STERCULIA FOETIDA
KK. Cotyledons not convolute; eophylls palmately lobed.
L. Eophylls mostly 7-lobate, the lobes serrate .... (Fig. 80) RICINUS COMMUNIS
LL. Eophylls mostly 3-5-lobate, the lobes not serrate .... (Fig. 81) ALEURITES MOLUCCANA
JJ. Eophylls bifoliolate, pinnate, or decompound.
M. Eophylls bifoliolate .... (Fig. 46) BAUHINIA sp.
MM. Eophylls pinnate or decompound.
N. Cotyledons deeply retuse; leaflets dentate .... (Fig. 171) JACARANDA MIMOSIFOLIA
NN. Cotyledons entire; leaflets entire.
O. First eophyll with four leaflets.
P. Second eophyll paripinnate .... (Fig. 47) CASSIA SIAMEA
PP. Second eophyll decompound .... (Fig. 38) PITHECELLOBIUM SAMAN
OO. First eophyll with more than four leaflets.
Q. First and second eophyll pinnate; seeds twice as long as broad .... (Fig. 50) DELONIX REGIA
QQ. First or second eophyll decompound; seeds not twice as long as broad.
R. First eophyll 1-pinnate; second eophyll 2-pinnate .... (Fig. 43) ALBIZIA LEBBECK

RR. First or second eophyll decompound with more than two pinnae.

S. Seeds ocellate; first eophyll pinnate; eglandular ....(Fig. 44) ENTEROLOBIUM CYCLOCARPUM

SS. Seeds not ocellate; first eophyll decompound, glandular ....(Fig. 45) PARKIA BIGLANDULOSA

HH. First eophylls simple or pennilobed.

T. First eophylls dentate or pennilobed; plants laticiferous or pellucid-punctate.

U. Latex present; cotyledons entire, not punctate.

V. Metaphylls pennilobed ....CARICA PAPAYA

VV. Metaphylls palmilobed ........COCHLOSPERMUM VITIFOLIUM

UU. Latex absent; cotyledons often dentate, pellucid-punctate ....(Fig. 64) CITRUS PARADISI

TT. First eophylls entire, or rarely denticulate or serrate; latex absent.

W. Metaphylls opposite; cotyledons stipulate ....(Fig. 175) POSOQUERIA LATIFOLIA

WW. Metaphylls alternate.

X. Metaphylls palmately lobed or compound; cotyledons contortuplicate.

Y. Cotyledons subsessile; metaphylls palmately compound ....(Fig. 120) ADANSONIA DIGITATA

YY. Cotyledons long-petiolate; metaphylls palmately lobed ....(Fig. 121) CAVANILLESIA PLATANIFOLIA

XX. Metaphylls simple or imparipinnate; cotyledons not contortuplicate.

Z. Eophylls exstipulate, aromatic ....(Fig. 19) ANNONA SQUAMOSA

ZZ. Eophylls stipulate, not aromatic.

a. Cotyledons long-petiolate; eophylls plinerved ....(Fig. 110) ZIZYPHUS JUJUBA

aa. Cotyledons subsessile; eophylls penninerved.

b. Cotyledons suborbicular, plinerved; eophylls broadly ovate to suborbicular ....(Fig. 59) GLIRICIDIA SEPIUM

bb. Cotyledons narrowly ovate, penninerved; eophylls narrowly ovate ....(Fig. 53) PTEROCARPUS INDICUS

APPENDIX 1.

Botanical names, Spanish names, figure references, and forest types for the species studied.

Botanical name	*Spanish name*	*Fig.*	*Forest*[4] *Type*
Acacia farnesiana (L.) Willd.	Aroma	40	3
Acrocomia media O. F. Cook	Corozo	6	5
Adansonia digitata L.	Baobab	120	8
Adenanthera pavonina L.	Peronillas	39	4,5
Albizia lebbeck (L.) Benth.	Acacia amarilla	43	8

[4] 1 = mangrove woodlands; 2 = littoral woodlands; 3 = dry limestone forests; 4 = dry coastal forests; 5 = moist coastal and moist limestone forests; 6 = lower cordillera and lower Luquillo forests; 7 = upper cordillera and upper Luquillo forests; 8 = gardens and parks.

Botanical name	Spanish name	Fig.	Forest[1] Type
Alchornea latifolia Sw.	Achiotillo	82	5,6,7
Alchorneopsis portoricensis Urban	Palo de gallina	85	6,7
Aleurites moluccana (L.) Willd.	Nuez de India	81	8
Allophylus crassinervis Radlk.	Gaetilla	101	5,6
Amyris elemifera L.	Tea	65	3
Anacardium occidentale L.	Pajuil	90	4,5,8
Andira inermis (W. Wright) H. B. K.	Moca	55	4,5,6
Annona squamosa L.	Anón	19	8
Ardisia glauciflora Urban	Ausubón	147	6
Artocarpus heterophyllus Lam.	Jaca	12	8
Avicennia germinans (L.) L. (*Avicennia nitida* Jacq.)	Mangle prieto	166	1
Bauhinia sp.	Mariposa	46	8
Bocconia frutescens L.	Palo de pan cimarrón	28	4,5,6
Bourreria succulenta Jacq.	Palo de vaca	none	3,4
Buchenavia capitata (Vahl) Eichl.	Granadillo	139	5,6
Bucida buceras L.	Ucar	135	3,4,5
Bumelia obovata (Lam.) A. DC.	Caimitillo	150	4
Bursera simaruba (L.) Sarg.	Almácigo	69	2,3,4,5
Byrsonima coriacea (Sw.) DC.	Maricao	63	3,4,5,6
Calophyllum calaba L. (*Calophyllum brasiliense* Camb.)	María	125	3,4,5,6
Calotropis procera (Ait.) R. Br.	Bomba	157	2,3
Calycogonium squamulosum Cogn.	Jusillo	none	7
Capparis coccolobifolia Mart.	Burro	27	3
Capparis cynophallophora L.	Burro prieto	26	2,3,4
Carica papaya L.	Lechosa	none	8
Casearia arborea (L. C. Rich.) Urban	Rabo ratón	131	4,5,6
Casearia guianensis (Aubl.) Urban	Palo blanco	128	5,6
Casearia sylvestris Sw.	Cafecíllo	130	4,5,6
Cassia siamea Lam.	Casia de Siam	47	8
Cassine xylocarpa Vent.	Coscorrón	96	2,4
Casuarina equisetifolia L.	Casuarina	7	2,4,5
Cavanillesia platanifolia (Humb. & Bonpl.) H. B. K.	Cuipo	121	8
Cecropia peltata L.	Yagruma hembra	13	4,5,6
Ceiba pentandra (L.) Gaertn.	Ceiba	118	3,4,5
Cestrum macrophyllum Vent.	Galán del monte	164	5,6
Chrysobalanus icaco L.	Icaco	35	2,4
Cissampelos pareira L.	Bejuco de mona	17	5,6
Citharexylum fruticosum L.	Péndula	165	1,2,3,4,5,6
Citrus paradisi MacFadyen	Toronja	64	8
Citrus spp.		none	8
Clusia sp.	Cupey, Cupeíllo	127	1,2,4,5,6,7
Coccoloba pyrifolia Desf.	Uvera	16	5,6
Coccoloba uvifera (L.) L.	Uva de playa	18	2
Cochlospermum vitifolium (Willd.) Spreng.	Rosa imperial	none	8
Cocos nucifera L.	Palma de coco	5	2,4,5
Coffea arabica L.	Café	182	5,6
Colubrina arborescens (Mill.) Sarg.	Abeyuelo	109	3,4
Comocladia glabra (Schultes) Spreng.	Carrasco	91	6
Conocarpus erectus L.	Mangle botón	133	1,2
Cordia alliodora (Ruiz & Pavón) Oken	Capá prieto	none	4,5,6
Cordia borinquensis Urban	Muñeco	163	6
Cordia lima (Desv.) Roem. & Schult.	Lija	161	6
Cordia nitida Vahl	Capá colorado	159	4

Botanical name	Spanish name	Fig.	Forest[4] Type
Cordia sulcata DC.	Moral	160	5,6
Crescentia cujete L.	Higuero	170	3,4
Croton lucida L.	Corchillo	83	3
Croton poecilanthus Urban	Sabinón	88	6,7
Cupania americana L.	Guara	102	5,6
Cyrilla racemiflora L.	Palo colorado	98	6,7
Dacryodes excelsa Vahl	Tabonuco	71	6
Daphnopsis philippiana Krug & Urban	Majagua brava	132	6,7
Delonix regia (Bojer) Raf.	Flamboyán	50	8
Dendropanax arboreus (L.) Decne. & Planch.	Pollo	148	5,6
Didymopanax morototoni (Aubl.) Decne. & Planch.	Yagrumo macho	144	5,6
Dodonaea viscosa (L.) Jacq.	Guitarán	104	2
Drypetes glauca Vahl	Varital	87	6
Enterolobium cyclocarpum (Jacq.) Griseb.	Guanacaste	44	8
Erythrina crista-galli L.	Cresta de gallo	60	8
Erythrina cf. *poeppigiana* (Walp.) O. F. Cook	Bucayo gigante	61	5,6
Erythroxylon areolatum L.	Indio	62	3,4
Eugenia borinquensis Britton	Guayabota	145	7
Eugenia jambos L.	Pomarrosa	143	2,4,5,6
Eugenia stahlii (Kiaersk.) Krug & Urban	Guayabota	141	6,7
Exostema caribaeum (Jacq.) Roem. & Schult.	Albarillo	179	3
Ficus citrifolia Mill. (*Ficus laevigata* Vahl)	Jagüey	11	3,4,5,6
Garcinia mangostana L.	Mangostán	126	8
Genipa americana L.	Jagua	180	4,5,6
Gliricidia sepium (Jacq.) Steud.	Mata-ratón	59	8
Gomidesia lindeniana Berg.	Cieneguillo	138	5,6
Gossypium arboreum L.	Algodón	122	3
Guaiacum officinale L.	Guayacán	none	3,4
Guaiacum sanctum L.	Guayacán blanco	70	3,4
Guatteria caribaea Urban	Haya blanca	15	6
Guarea guidonia (L.) Sleumer (*Guarea trichilioides* L.)	Guaraguao	74	5,6
Guarea ramiflora Vent.	Guaraguaillo	77	6
Guettarda sp.	Cucubano	176	3,4,5,6
Haematoxylon campechianum L.	Campeche	49	3
Haenianthus salicifolius var. *obovatus* (Krug & Urb.) Standl.	Caney	155	7
Hernandia sonora L.	Mago	21	4,5,6
Heteropteris laurifolia (L.) A. Juss.	Bejuco de buey	67	5,6
Heterotrichum cymosum (Wendl.) Urban	Camasey peludo	none	6,7
Hevea brasiliensis (H. B. K.) Muell.-Arg.	Goma del Pará	76	8
Hibiscus tiliaceus L.	Emajagua	114	1,2,3,4,5,6,
Hillia parasitica Jacq.	Himencillo	173	7
Hirtella rugosa Pers.	Icaquillo	36	6
Homalium racemosum Jacq.	Caracolillo	129	3,4,5,6
Hura crepitans L.	Molinillo	86	4,5
Hymenaea courbaril L.	Algarrobo	48	4,5,6
Ilex nitida (Vahl) Maxim.	Briqueta	92	6

Botanical name	Spanish name	Fig.	Forest[1] Type
Inga fagifolia (L.) Willd. (*Inga laurina* [Sw.] Willd.)	Guamá	32	5,6
Inga vera Willd.	Guava	34	5,6
Ipomoea pes-caprae (L.) Roth.	Bejuco de playa	152	2
Ixora ferrea (Jacq.) Benth.	Palo clavo	181	6
Jacaranda mimosifolia D. Don	Jacaranda	171	8
Jatropha gossypifolia L.	Frailecillo	79	8
Laguncularia racemosa (L.) Gaertn. f.	Mangle blanco	136	1
Lasianthus lanceolatus (Griseb.) Urban	Mata de peo	none	6,7
Leucaena leucocephala (Lam.) De Wit (*Leucaena glauca* (L.) Benth.)	Zarcilla	42	3,4
Linociera domingensis (Lam.) Knobl.	Hueso blanco	154	5,6
Machaerium lunatum (L.) Ducke	Escambrón	58	1
Mangifera indica L.	Mango	94	4,5,6,8
Manilkara balata (Aubl.) Dubard (*Manilkara bidentata* (A.DC.) Chev.)	Ausubo	149	1,2,4,5,6
Matayba domingensis (DC.) Radlk.	Negra lora	106	7
Melia azedarach L.	Alelaila	none	8
Meliococcus bijugatus Jacq.	Quenepa	107	4,5,6,8
Meliosma herbertii Rolfe	Aguacatillo	108	6,7
Miconia spp.	Camasey	none	5,6
Micropholis chrysophylloides Pierre	Caimitillo	none	5,6,7
Micropholis garciniaefolia Pierre	Caimitillo verde	151	7
Montezuma speciosissima Sessé & Moc.	Maga	115	5,6,8
Moringa oleifera Lam.	Resedá	29	3,4
Myrcia splendens (Sw.) DC.	Hoja menuda	140	4,5,6
Nectandra antillana Meisn.	Aguacatillo	22	5
Ochroma pyramidale (Cav. ex Lam.) Urban	Guano	119	4,5,6
Ocotea leucoxylon (Sw.) Mez	Laurel geo	24	5,6
Ocotea moschata (Meisn.) Mez	Nuez moscada	25	6,7
Ocotea spathulata Mez	Nemocá	30	6,7
Ormosia krugii Urban	Palo de matos	56	6
Pachira aquatica Aubl.	Ceiba de agua	none	8
Palicourea alpina (Sw.) DC.	Cachimbo	178	6
Parkia biglandulosa W. & A.	Uya	45	8
Parkinsonia aculeata L.	Palo de rayo	51	3,4
Paullinia pinnata L.	Bejuco de palma	105	5,6
Persea americana Mill.	Aguacate	23	4,5,6,8
Pictetia aculeata (Vahl) Urban	Tachuelo	57	3,4
Piper aduncum L.	Higuillo	10	5,6,7
Piper treleaseanum Britton & Wilson	Higuillo blanco	9	6
Pithecellobium arboreum (L.) Urban	Cojoba	33	5,6
Pithecellobium dulce (Roxb.) Benth.	Guamuchil	none	8
Pithecellobium saman (Jacq.) Benth.	Samán	38	4,5,6,8
Pithecellobium unguis-cati (L.) Benth.	Uña de gato	37	3
Plumeria alba L.	Alelí	158	3
Plumeria obtusa L.	Alelí cimarrón	156	4,5,6
Podocarpus coriaceus L. C. Rich.	Caobilla	1	5,7
Posoqueria latifolia (Rudge) R. & S.	Borajo	175	8
Pouteria multiflora (A. DC.) Eyma	Jácana	153	5,6,8
Prestoea montana (Graham) Nicholson (*Euterpe globosa* Auct.)	Palma de sierra	4	6,7
Prosopis juliflora (Sw.) DC.	Bayahonda	41	3,4
Psidium guajava L.	Guayaba	137	4,5,6
Psychotria berteriana DC.	Cachimbo	174	6

Botanical name	*Spanish name*	*Fig.*	*Forest*[1] *Type*
Psychotria maleolens Urban	Peo de gato	none	6,7
Pterocarpus indicus Willd.	Pterocarpus	53	8
Pterocarpus officinalis Jacq.	Palo de pollo	54	1,5
Quararibea turbinata (Sw.) Poir.	Garrocho	117	3,4,5,6
Rapanea ferruginea (Ruiz & Pav.) Mez	Mantequero	146	6
Rheedia portoricensis Urban	Palo de cruz	124	2,4,5,6
Rhizophora mangle L.	Mangle colorado	142	1
Ricinus communis L.	Higuereta	80	8
Rourea surinamensis Miq.	Juan caliente	31	6
Roystonea borinquena O. F. Cook	Palma real	3	1,2,3,4,5,6,8
Sabal causiarum (O. F. Cook) Beccari	Palma de sombrero	2	4
Sapindus saponaria L.	Jaboncillo	99	3,4,5
Sapium laurocerasus Desf.	Tabaiba	84	5,6
Savia sessiliflora (Sw.) Willd.	Aretillo	89	3
Schaefferia frutescens Jacq.	Jiba	95	4
Securidaca diversifolia (L.) S. F. Blake	Bejuco de sopla	78	5,6
Serjania polyphylla (L.) Radlk.	Bejuco de costilla	100	3
Sloanea berteriana Choisy	Motillo	113	6
Smilax cf. *coriacea* Spreng.	Dunguey	8	5,6
Spathodea campanulata Beauv.	Tulipán	169	4,5
Spondias purpurea L.	Ciruela del país	93	4,5,6,8
Sterculia apetala (Jacq.) Karst.	Anacaguita	123	8
Sterculia foetida L.	Anacaguita	122	8
Swietenia macrophylla King	Caoba hondureña	72	5,6
Swietenia mahagoni Jacq.	Caoba dominicana	73	3,4
Tabebuia heterophylla (DC.) Britton	Roble blanco	167	2,3,4,5,6
Tabebuia rigida Urban	Roble de sierra	168	7
Tamarindus indica L.	Tamarindo	52	3,4
Tecoma stans (L.) H. B. K.	Roble amarillo	172	2
Tectona grandis L. f.	Teca	162	4,5,8
Terebraria resinosa (Vahl) Sprague	Aquilón	177	4,5
Terminalia catappa L.	Almendra	134	2,4,5
Tetragastris balsamifera (Sw.) Kuntze	Masa	68	6
Thespesia populnea (L.) Soland.	Emajagüilla	116	1,2,4,5,6
Thouinia portoricensis Radlk.	Serrasuela	103	3,4
Trichilia hirta L.	Tinacio	none	3,4
Trichilia pallida Sw.	Gaeta	75	5,6
Triumfetta sp.	Cadillo	111	5,6
Turpinia paniculata Vent.	Sauco cimarrón	97	5,6,7
Urera baccifera (L.) Gaud.	Ortega	14	6
Ximenia americana L.	Manzanilla	20	2,3
Zanthoxylum sp.	Aceitillo	66	4,5,6
Zizyphus jujuba (L.) Lam.	Aprines	110	3,8

Plate 1

1. *Podocarpus coriaceus* (× ¾). 2. *Sabal causiarum* (× ½). 3. *Roystonea borinquena* (× ½). 4. *Prestoea montana* (× ½). 5. *Cocos nucifera* (× ¼). 6. *Acrocomia media* (× ¼). 7. *Casuarina equisetifolia* (× 1). 8. *Smilax* cf. *coriacea* (× ½).

Plate 2

9. *Piper treleaseanum* (× ½). 10. *Piper aduncum* (× ½). 11. *Ficus citrifolia* (× ½). 12. *Artocarpus heterophyllus* (× ¼). 13. *Cecropia peltata* (× ½). 14. *Urera baccifera* (× ¾). 15. *Guatteria caribaea* (× ¾). 16. *Coccoloba pyrifolia* (× ¾). 17. *Cissampelos pareira* (× ¾). 18. *Coccoloba uvifera* (× ½). 19. *Annona squamosa* (a & b × ½). 20. *Ximenia americana* (× ½).

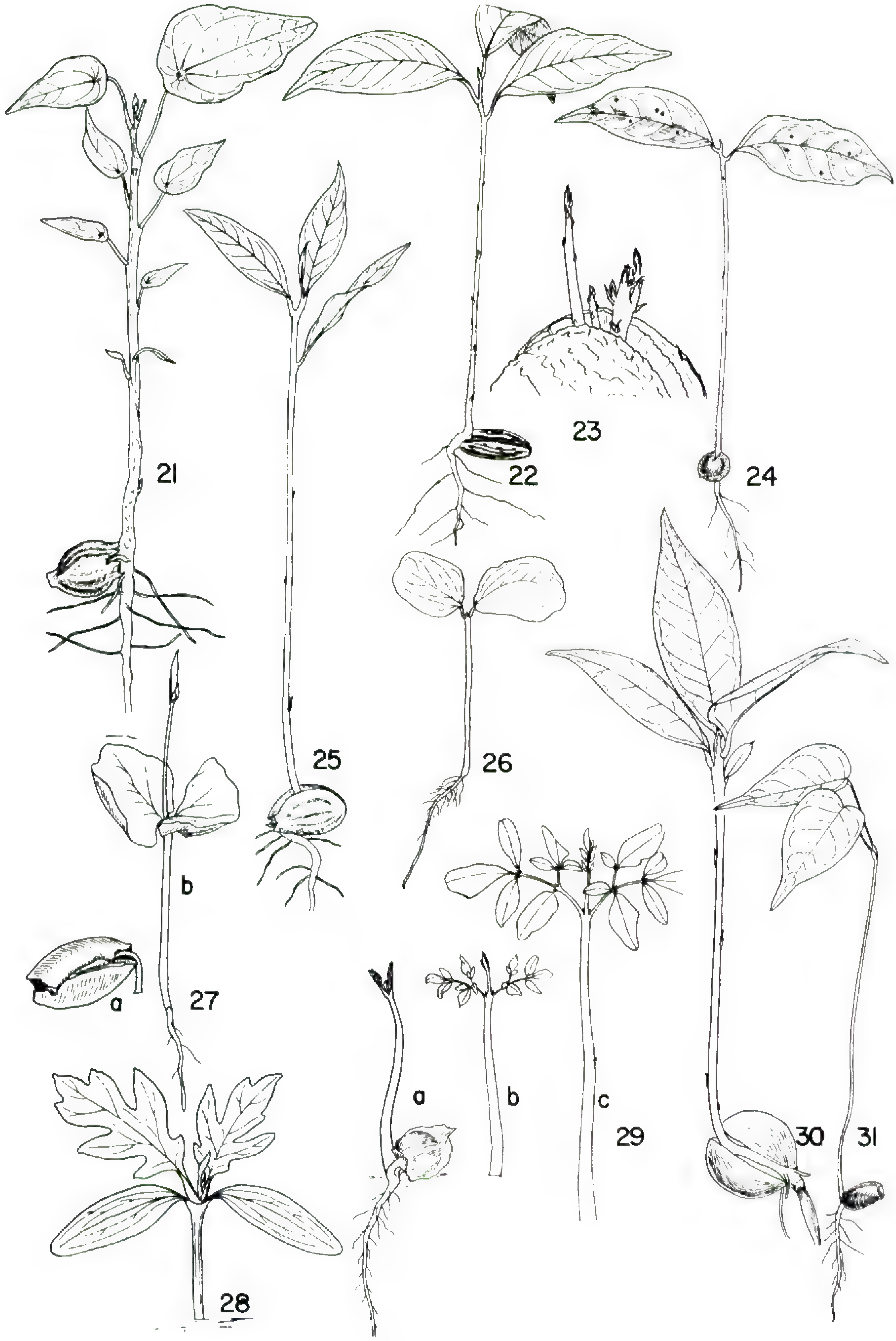

Plate 3

21. *Hernandia sonora* (× 1/3). 22. *Nectandra antillana* (× 1/2). 23. *Persea americana* (× 1/2). 24. *Ocotea leucoxylon* (× 1/2). 25. *Ocotea moschata* (× 1/4). 26. *Capparis cynophallophora* (× 1). 27. *Capparis coccolobifolia* (× 1). 28. *Bocconia frutescens* (× 1/2). 29. *Moringa oleifera* (a,b, & c × 1/2). 30. *Ocotea spathulata* (× 1/2). 31. *Rourea surinamensis* (× 1/2).

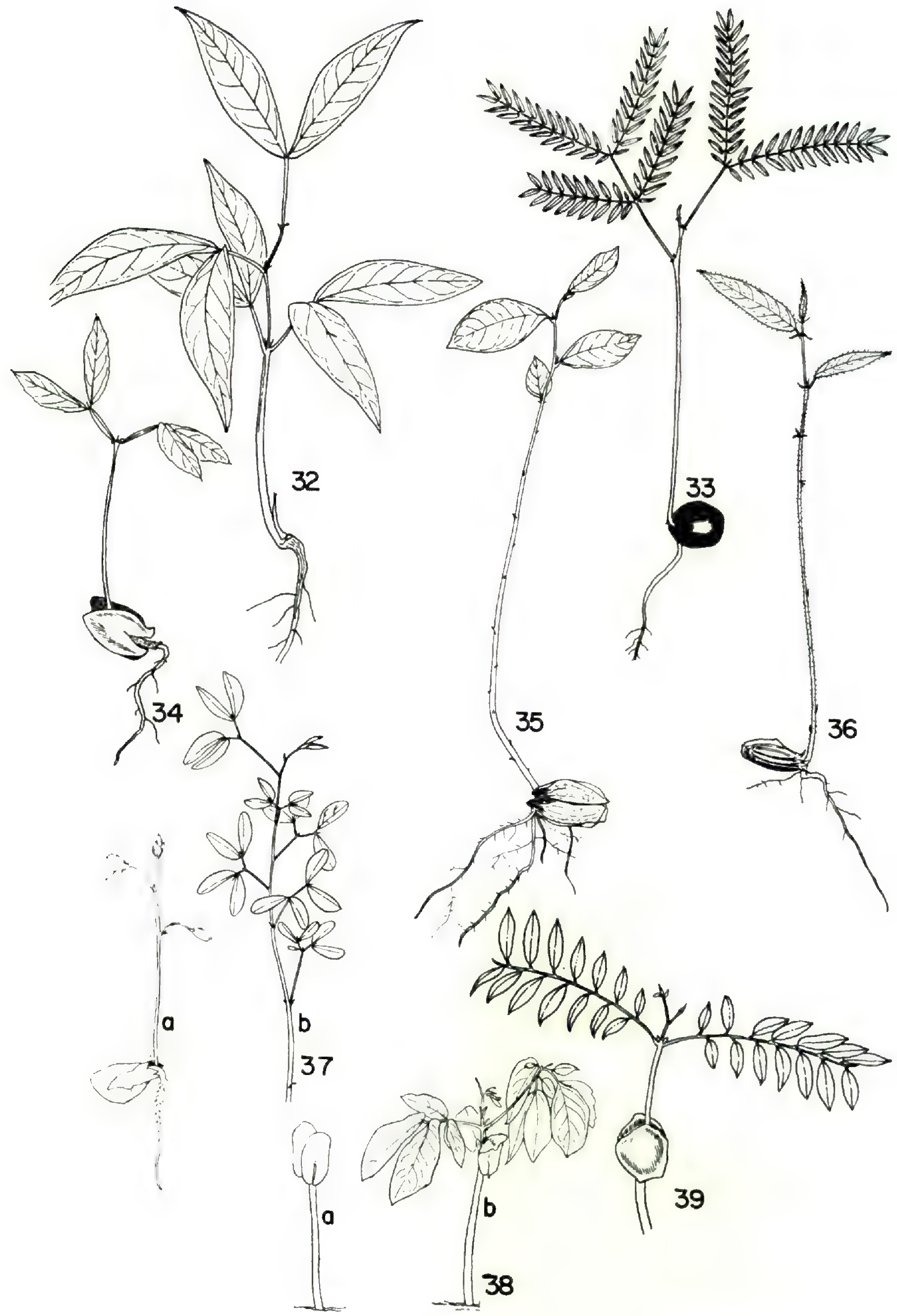

Plate 4

32. *Inga fagifolia* (× ¾). 33. *Pithecellobium arboreum* (× ½). 34. *Inga vera* (× ½). 35. *Chrysobalanus icaco* (× ½). 36. *Hirtella rugosa* (× ½). 37. *Pithecellobium unguis-cati* (a & b × 1). 38. *Pithecellobium saman* (× ½). 39. *Adenanthera pavonina* (× ½).

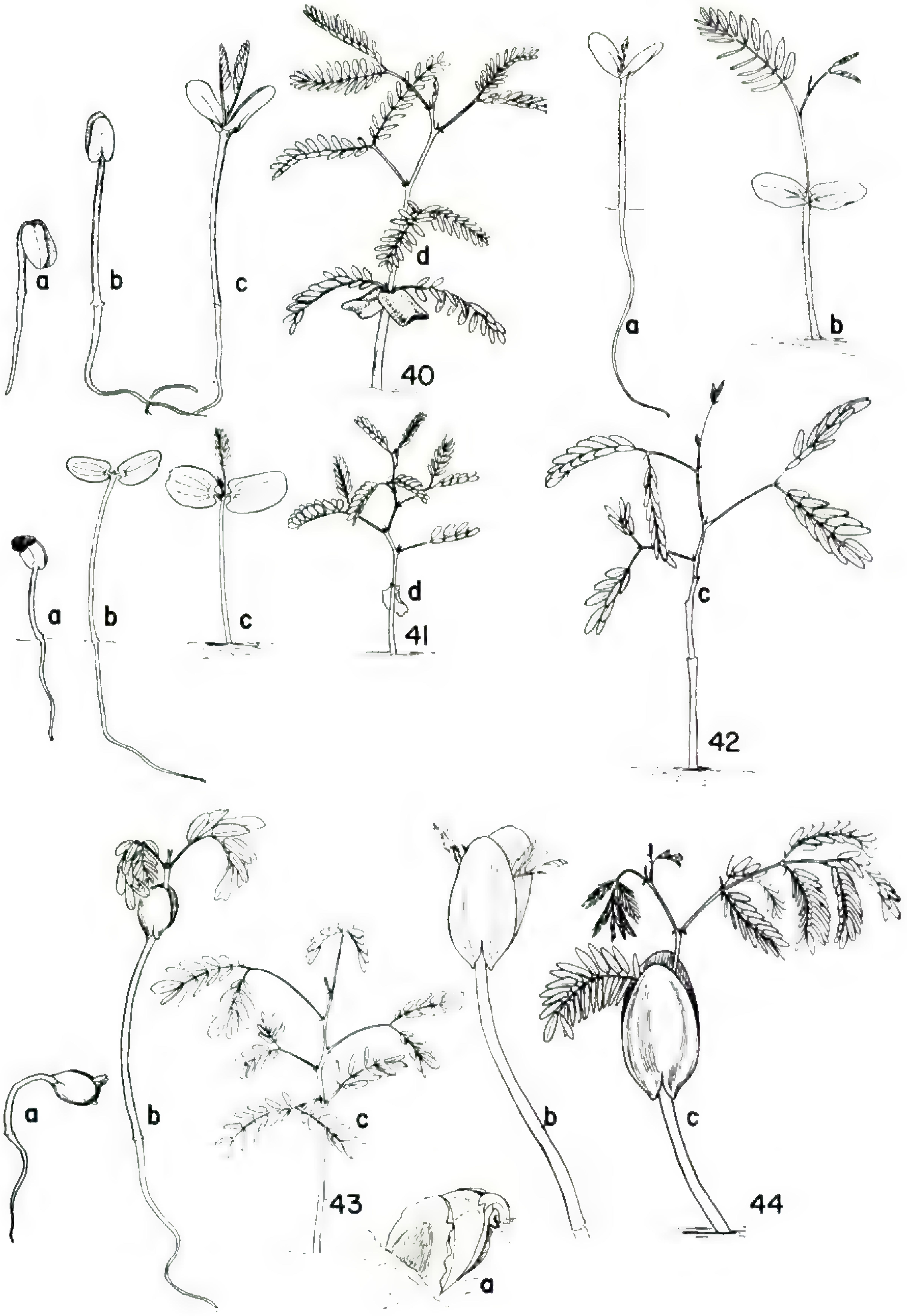

Plate 5

40. *Acacia farnesiana* (a,b,c, & d × ½). 41. *Prosopis juliflora* (a,b,c, & d × ½). 42. *Leucaena leucocephala* (a,b, & c × ½). 43. *Albizia lebbeck* (a,b, & c × ½). 44. *Enterolobium cyclocarpum* (a,b, & c × ½).

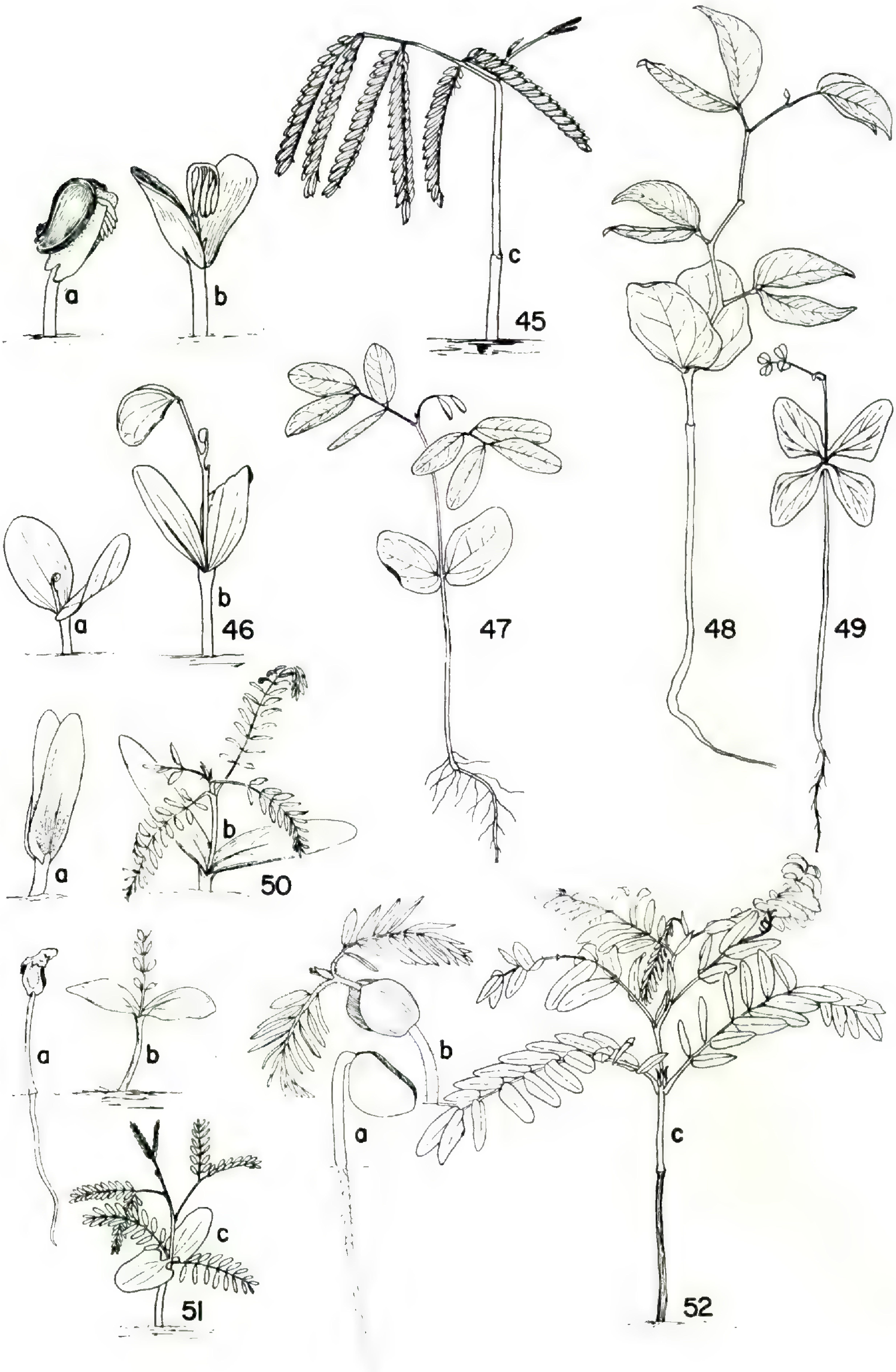

Plate 6

45. *Parkia biglandulosa* (a,b, & c × ½). 46. *Bauhinia* sp. (a & b × ¾). 47. *Cassia siamea* (× 1). 48. *Hymenaea courbaril* (× ½). 49. *Haematoxylon campechianum* (× 1). 50. *Delonix regia* (a & b × ½). 51. *Parkinsonia aculeata* (a,b, & c × ½). 52. *Tamarindus indica* (a,b, & c × ½).

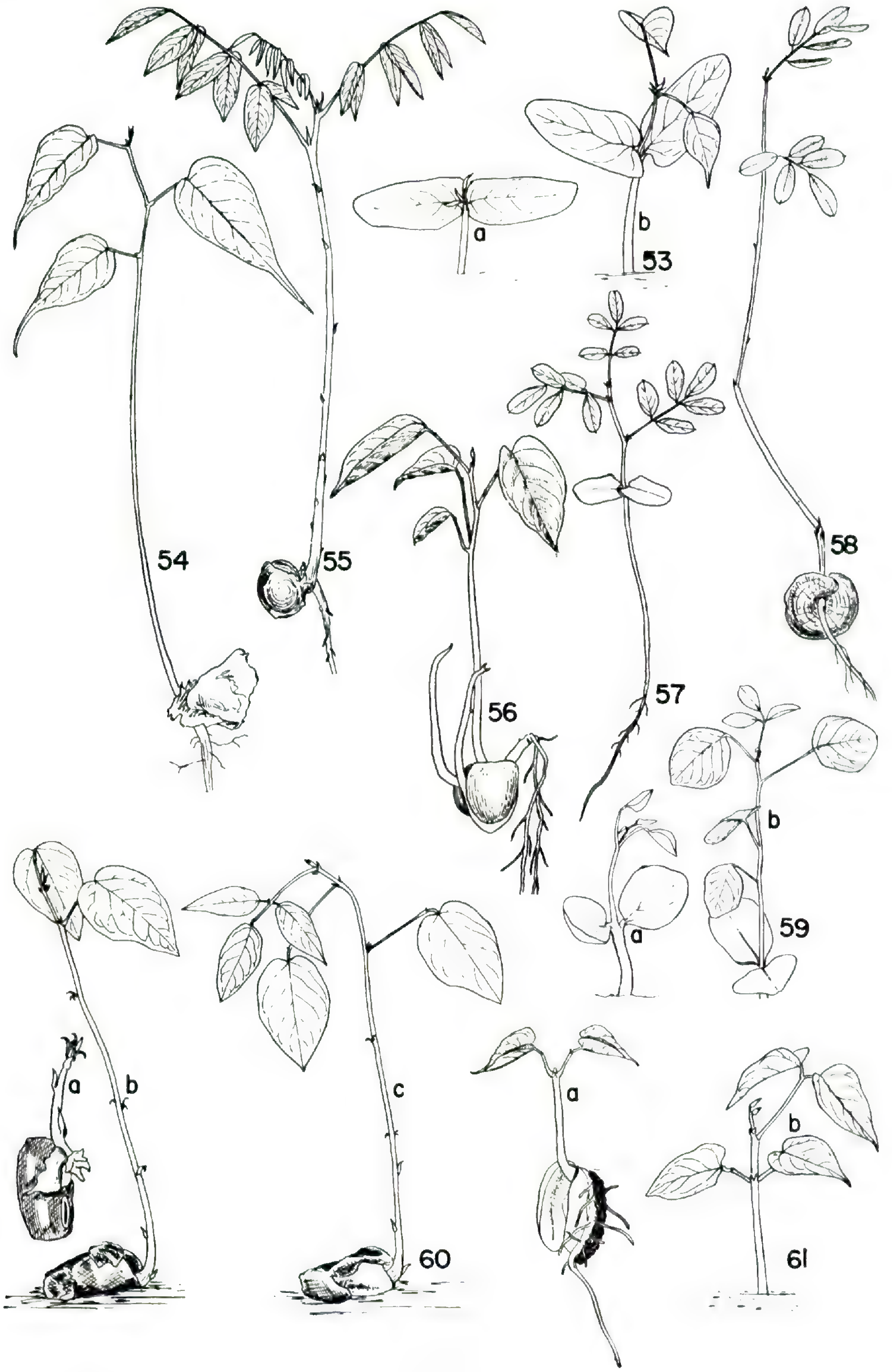

Plate 7

53. *Pterocarpus indicus* (a & b × ¾). 54. *Pterocarpus officinalis* (× ½). 55. *Andira inermis* (× ⅓). 56. *Ormosia krugii* (× ½). 57. *Pictetia aculeata* (× ¾). 58. *Machaerium lunatum* (× ¼). 59. *Gliricidia sepium* (a & b × ½). 60. *Erythrina crista-galli* (a,b, & c ⅓). 61. *Erythrina* cf. *poeppigiana* (a & b × ⅓).

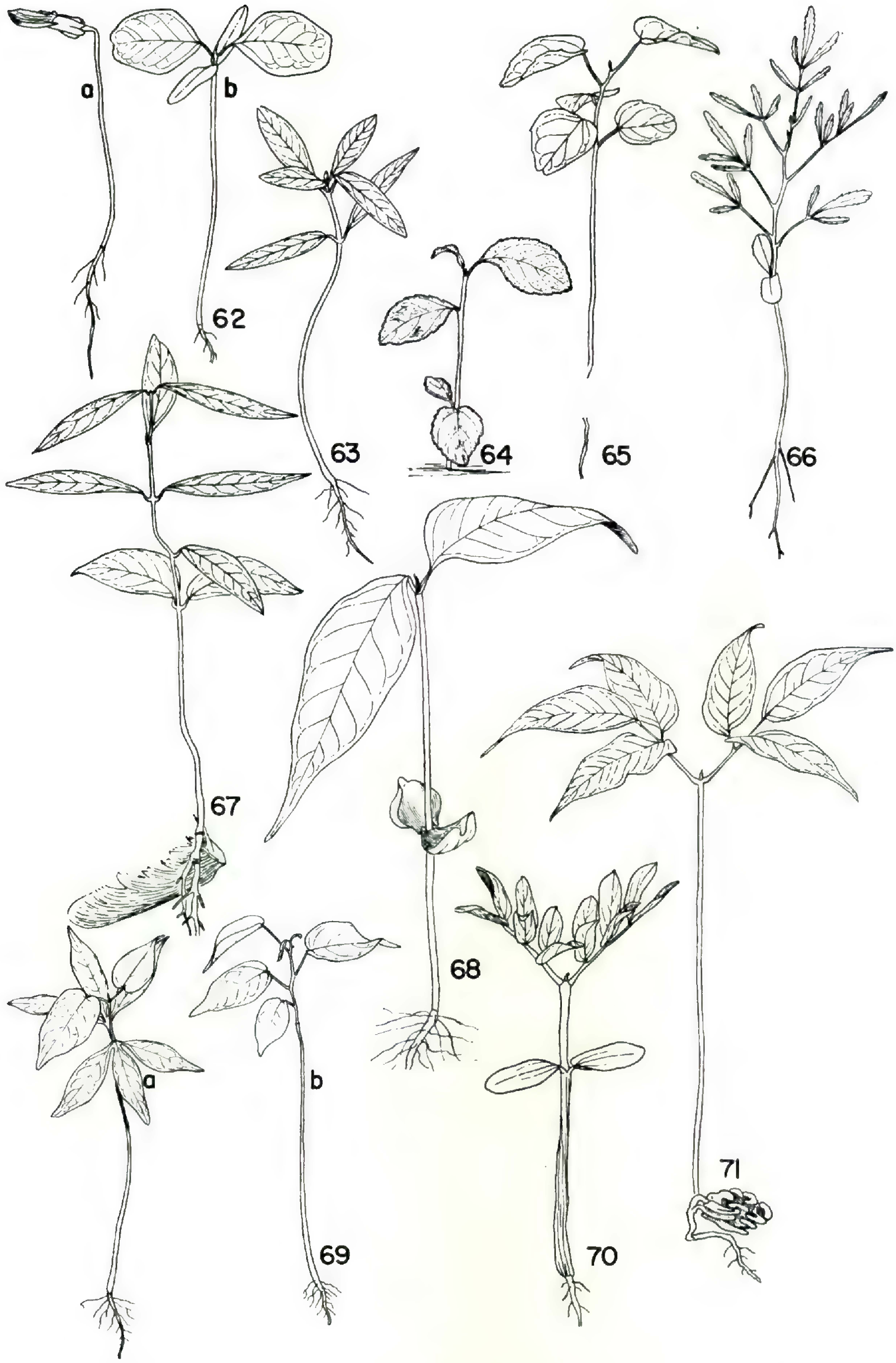

Plate 8

62. *Erythroxylon areolatum* (a & b × 1). 63. *Byrsonima coriacea* (× 3/4). 64. *Citrus paradisi* (× 1/2). 65. *Amyris elemifera* (× 1). 66. *Zanthoxylum* sp. (× 3/4). 67. *Heteropteris laurifolia* (× 1/2). 68. *Tetragastris balsamifera* (× 1/2). 69. *Bursera simaruba* (a & b × 1/3). 70. *Guaiacum sanctum* (× 3/4). 71. *Dacryodes excelsa* (× 1/2).

Plate 9

72. *Swietenia macrophylla* (a & b × ½). 73. *Swietenia mahagoni* (× ½). 74. *Guarea guidonia* (× ½). 75. *Trichilia pallida* (× ¾). 76. *Hevea brasiliensis* (× ¼). 77. *Guarea ramiflora* (× ½). 78. *Securidaca diversifolia* (× ⅝). 79. *Jatropha gossypifolia* (× ½).

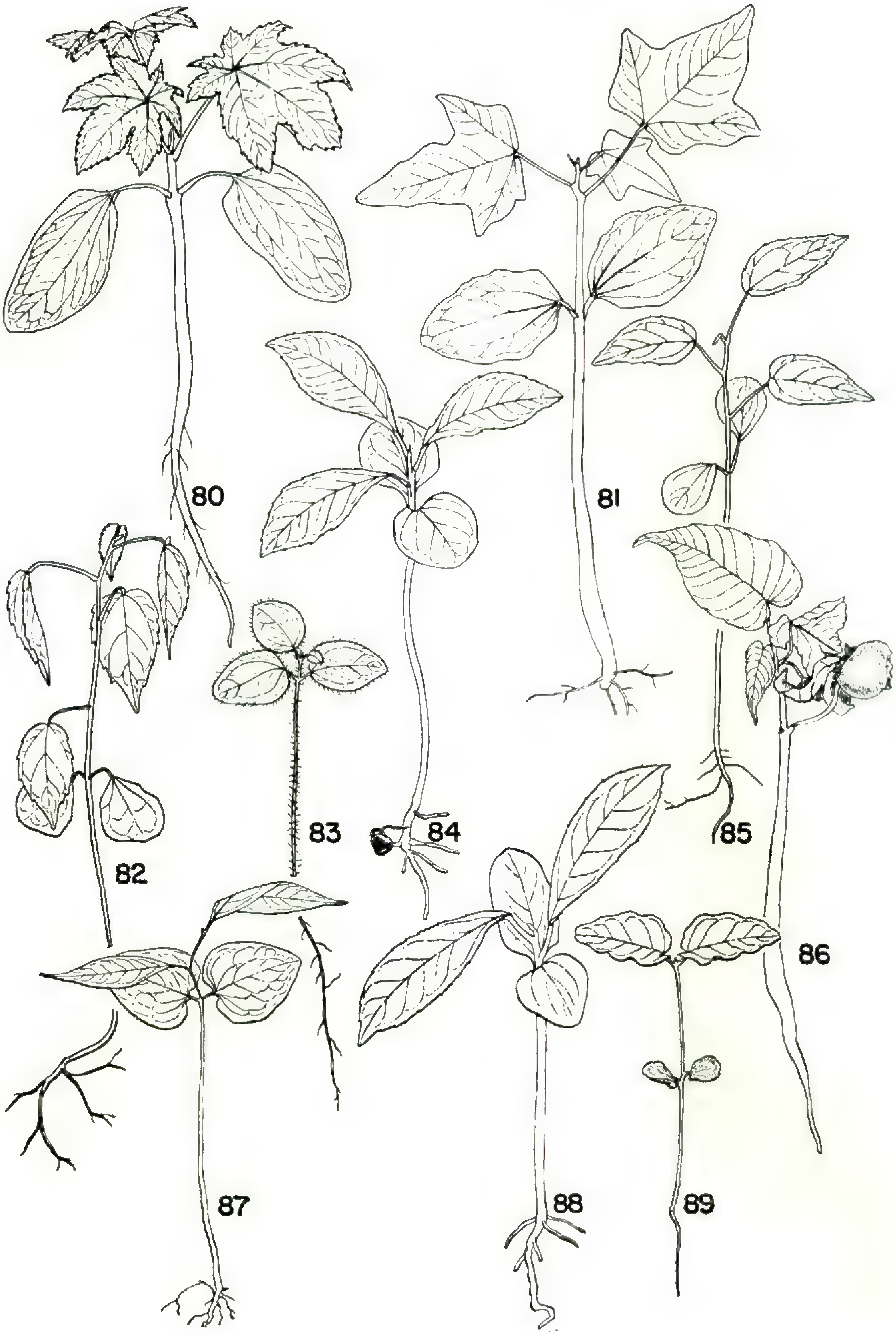

Plate 10

80. *Ricinus communis* (× ½). 81. *Aleurites moluccana* (× ⅓). 82. *Alchornea latifolia* (× ½). 83. *Croton lucida* (× 1-¼). 84. *Sapium laurocerasus* (× ½). 85. *Alchorneopsis portoricensis* (× ½). 86. *Hura crepitans* (× ½). 87. *Drypetes glauca* (× ½). 88. *Croton poecilanthus* (× ½). 89. *Savia sessiliflora* (× ¼).

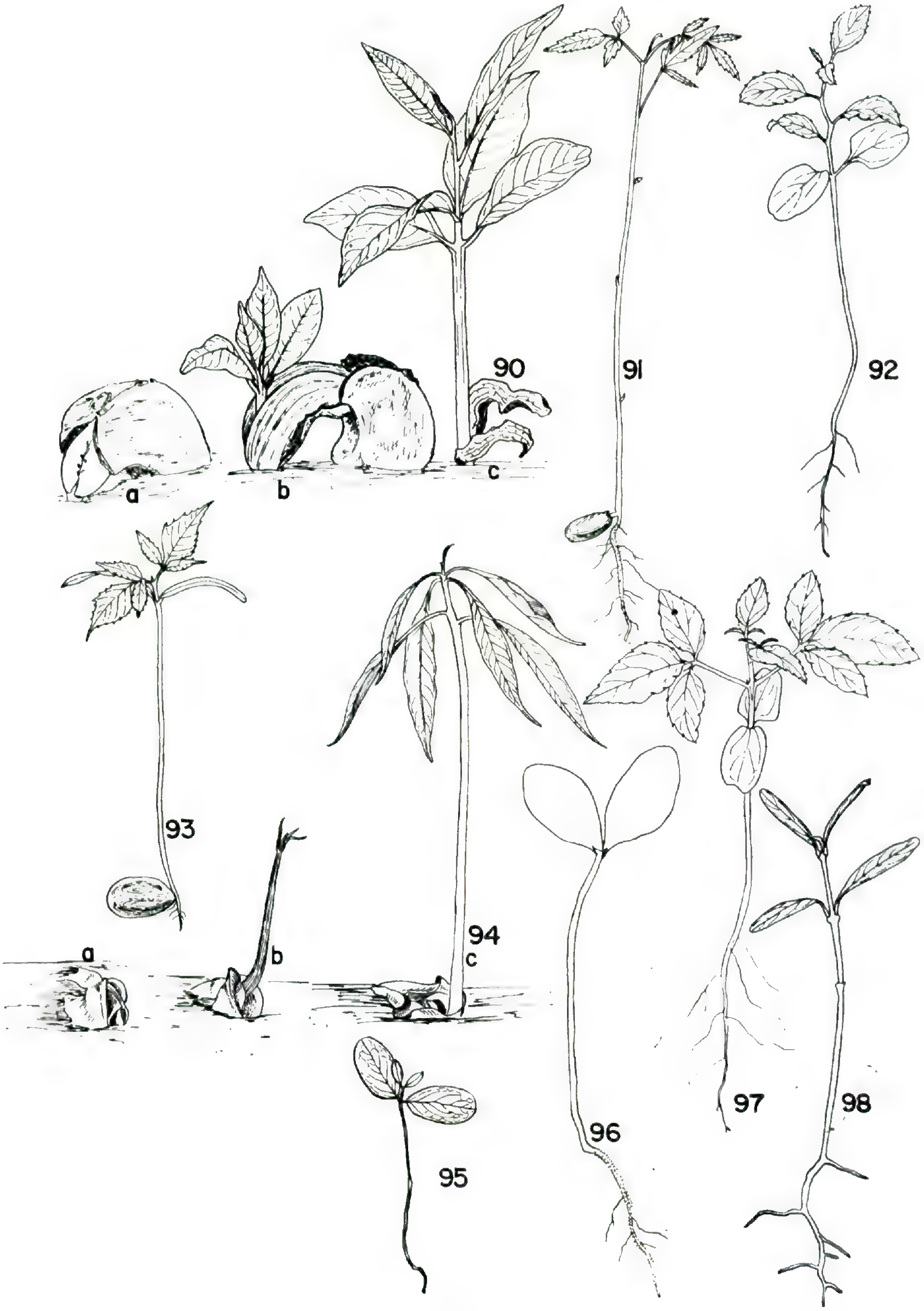

Plate 11

90. *Anacardium occidentale* (a & b × 2, c × 1). 91. *Comocladia glabra* (× ½). 92. *Ilex nitida* (× ¾). 93. *Spondias purpurea* (× ½). 94. *Mangifera indica* (a,b, & c × ¼). 95. *Schaefferia frutescens* (× 1). 96. *Cassine xylocarpa* (× ½). 97. *Turpinia paniculata* (× ⅝). 98. *Cyrilla racemiflora* (× 1).

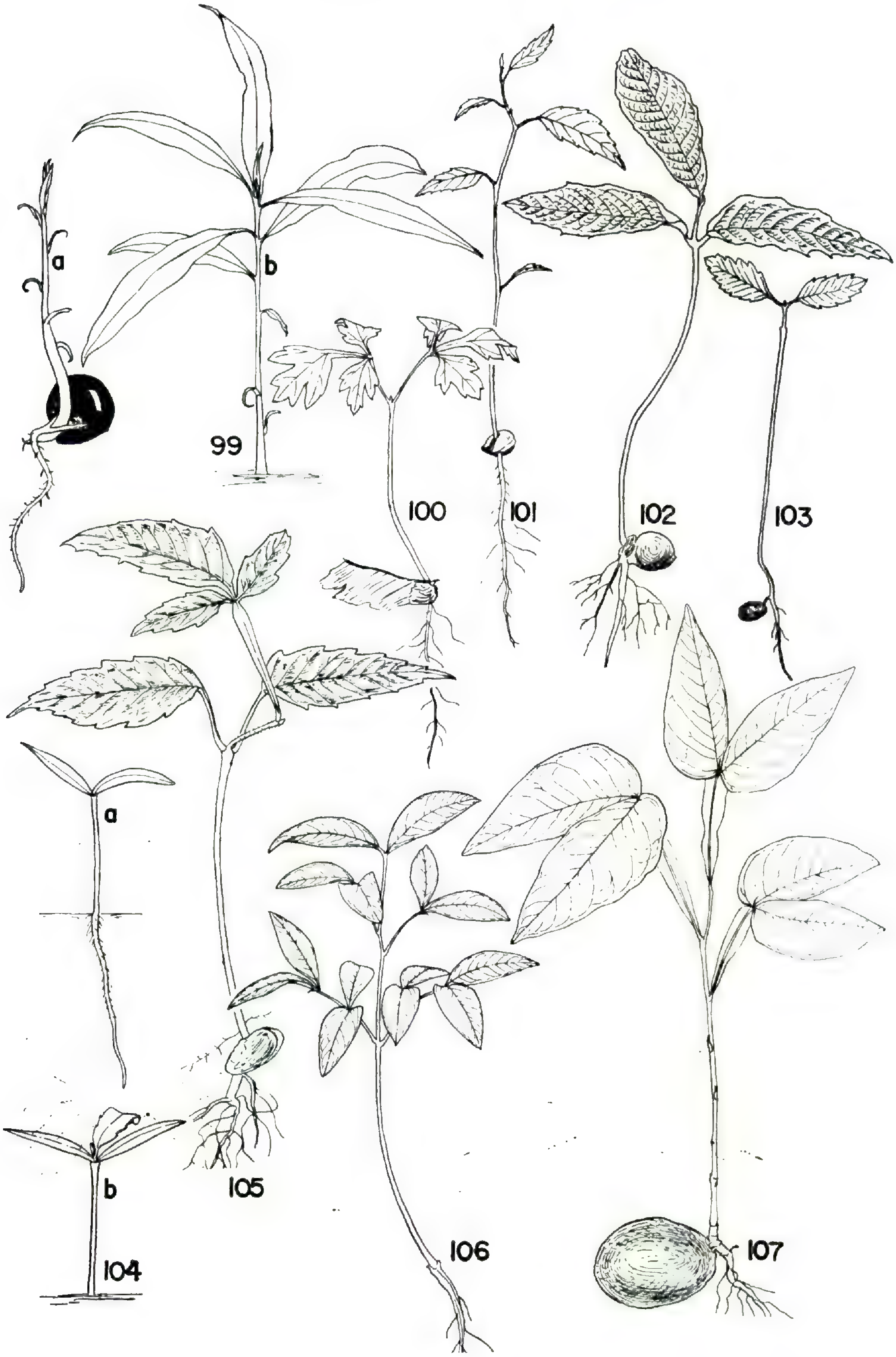

Plate 12

99. *Sapindus saponaria* (a & b × ½). 100. *Serjania polyphylla* (× ½). 101. *Allophylus crassinervis* (× ¾). 102. *Cupania americana* (× ½). 103. *Thouinia portoricensis* (× ½). 104. *Dodonaea viscosa* (a & b × ½). 105. *Paullinia pinnata* (× ½). 106. *Matayba domingensis* (× ¾). 107. *Melicoccus bijugatus* (× ½).

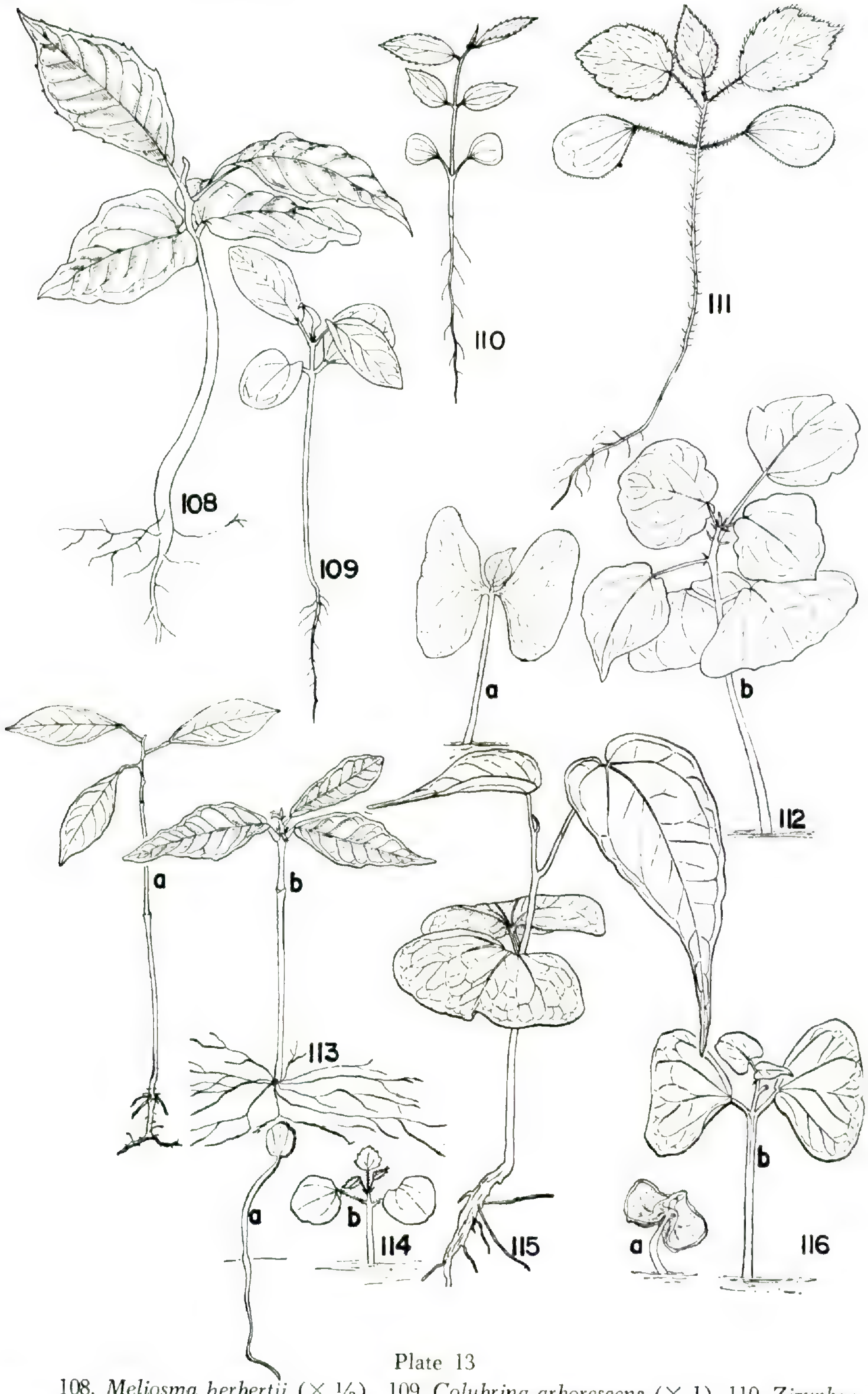

Plate 13

108. *Meliosma herbertii* (× ½). 109. *Colubrina arborescens* (× 1). 110. *Zizyphus jujuba* (× ½). 111. *Triumfetta sp.* (× 1-½). 112. *Gossypium arboreum* (a & b × ½). 113. *Sloanea berteriana* (a & b × ½). 114. *Hibiscus tiliaceus* (a & b × ½). 115. *Montezuma speciosissima* (× ½). 116. *Thespesia populnea* (a & b × ½).

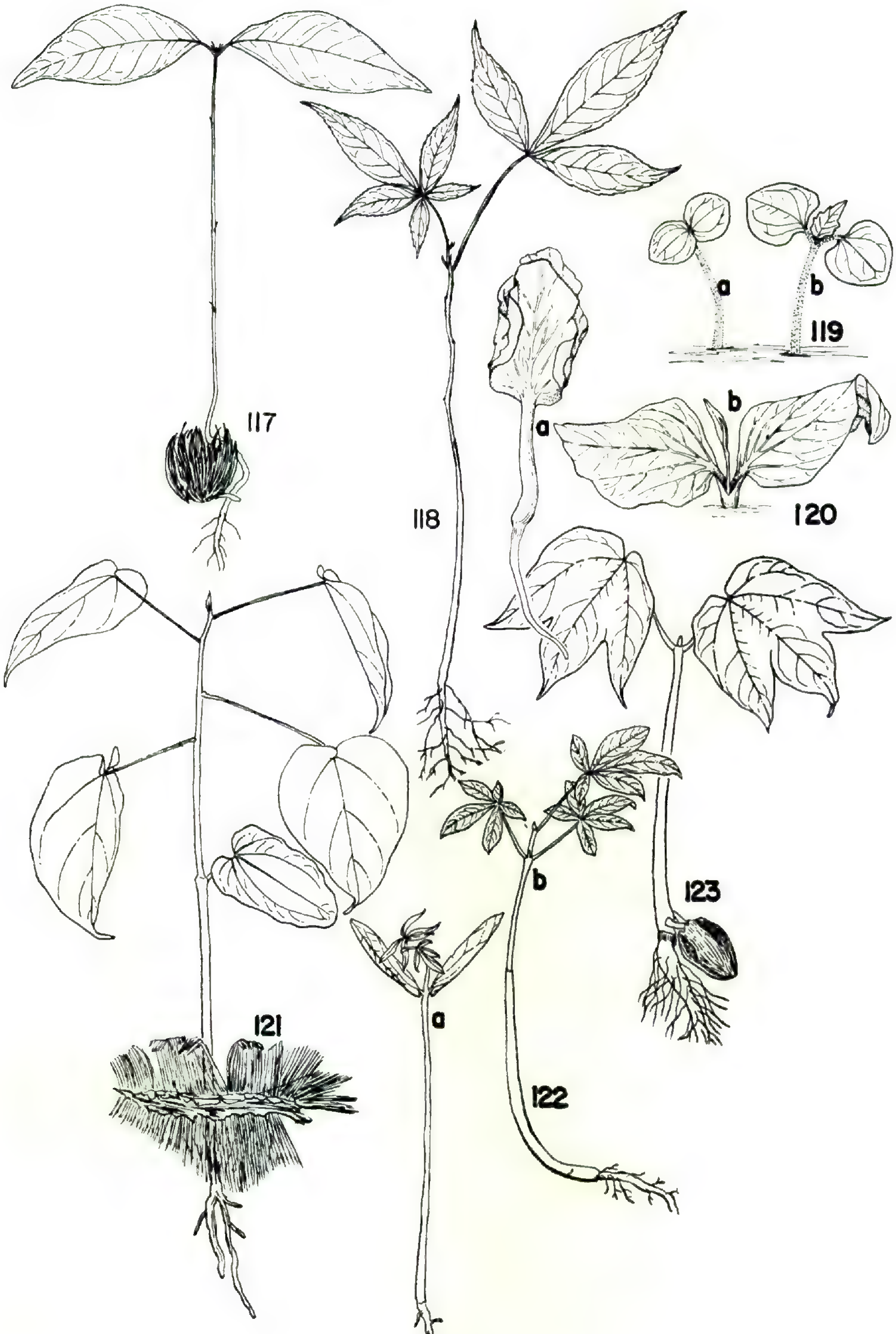

Plate 14

117. *Quararibea turbinata* (× ½). 118. *Ceiba pentandra* (× ½). 119. *Ochroma pyramidale* (a & b × 1). 120. *Adansonia digitata* (a & b × ½). 121. *Cavanillesia platanifolia* (× ⅜). 122. *Sterculia foetida* (a & b × ¼). 123. *Sterculia apetala* (× ⅓).

Plate 15

124. *Rheedia portoricensis* (× ½). 125. *Calophyllum calaba* (a & b × ½, c × ⅓). 126. *Garcinia mangostana* (× ½). 127. *Clusia* sp. (× 1). 128. *Casearia guianensis* (× 1). 129. *Homalium racemosum* (× 1). 130. *Casearia sylvestris* (× 1). 131. *Casearia arborea* (× 1). 132. *Daphnopsis philippiana* (× 1).

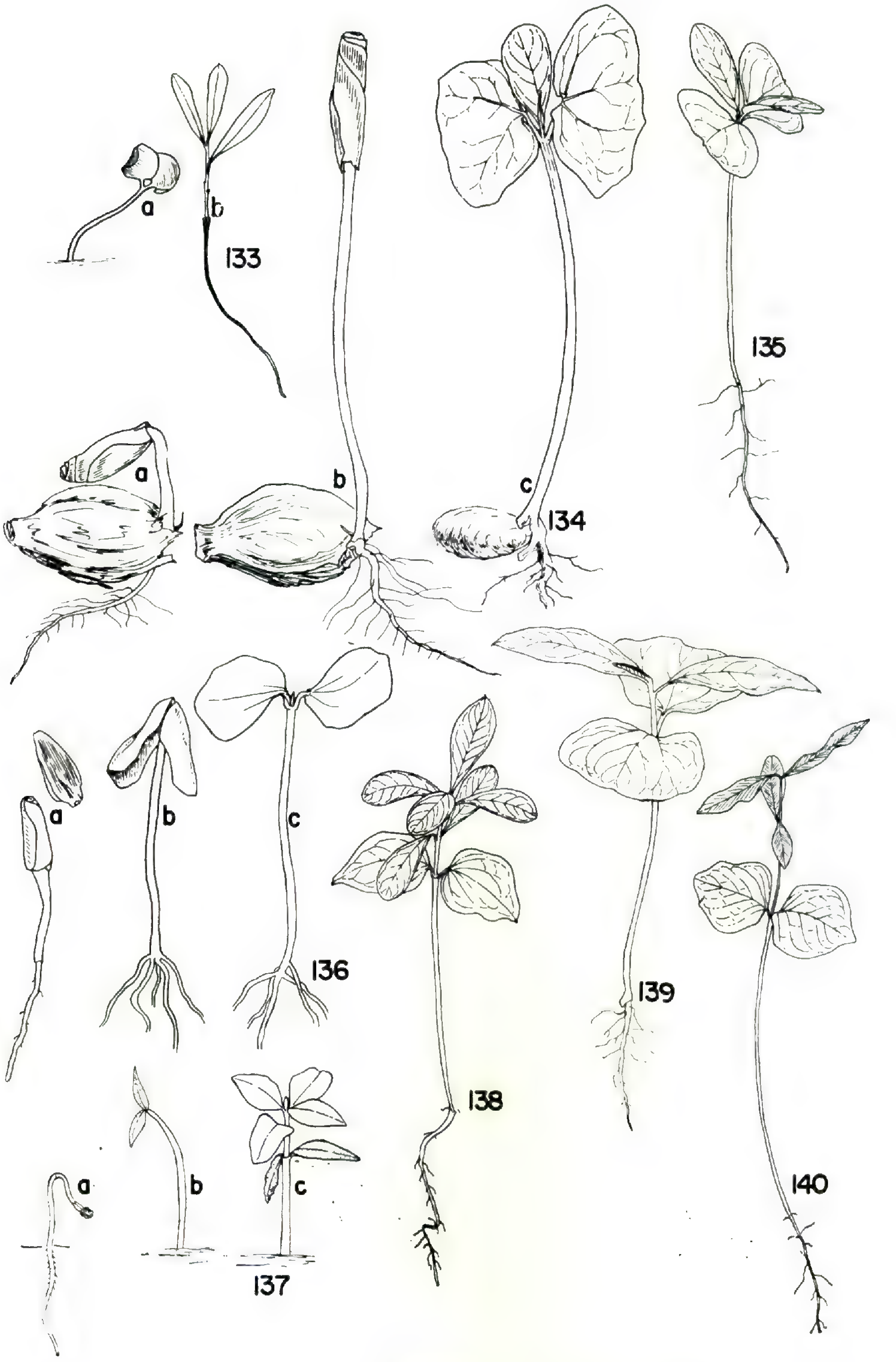

Plate 16

133. *Conocarpus erectus* (a × 1, b × ½). 134. *Terminalia catappa* (a,b, & c × ½). 135. *Bucida buceras* (× 1). 136. *Laguncularia racemosa* (a,b, & c × ½). 137. *Psidium guajava* (a,b, & c × 1). 138. *Gomidesia lindeniana* (× ½). 139. *Buchenavia capitata* (× ½). 140. *Myrcia splendens* (× ½).

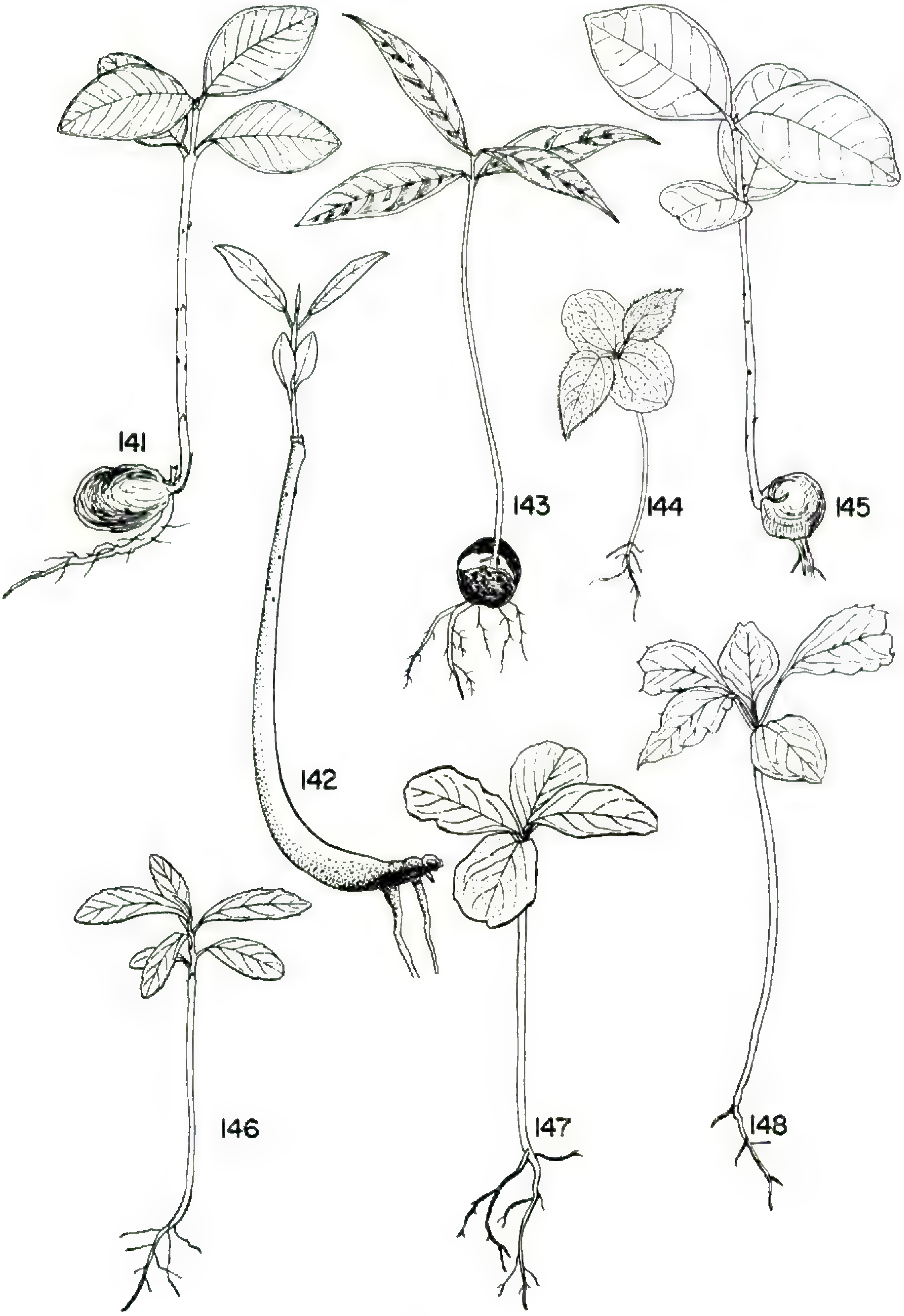

Plate 17

141. *Eugenia stahlii* (× ½). 142. *Rhizophora mangle* (× ⅓). 143. *Eugenia jambos* (× ½). 144. *Didymopanax morototoni* (× ½). 145. *Eugenia borinquensis* (× ½). 146. *Rapanea ferruginea* (× 1). 147. *Ardisia glauciflora* (× 1). 148. *Dendropanax arboreus* (× ⅝).

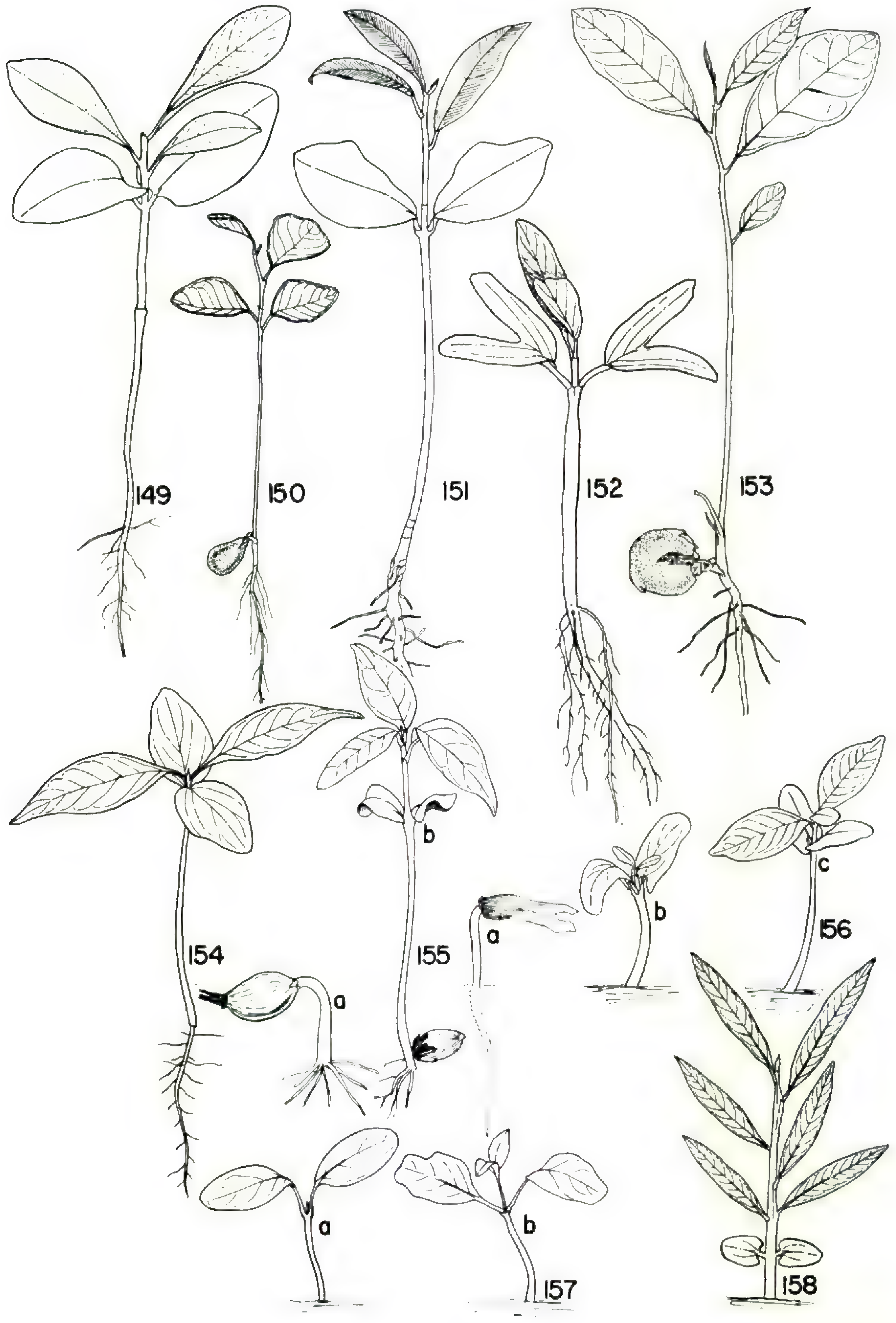

Plate 18

149. *Manilkara balata* (× ½). 150. *Bumelia obovata* (× ¾). 151. *Micropholis garciniaefolia* (× ½). 152. *Ipomoea pes-caprae* (× ½). 153. *Pouteria multiflora* (× ¼). 154. *Linociera domingensis* (× ¾). 155. *Haenianthus salicifolius* var. *obovatus* (a × ⅝, b × ⅜). 156. *Plumeria obtusa* (a,b, & c × ½). 157. *Calotropis procera* (a & b × ½). 158. *Plumeria alba* (× ½).

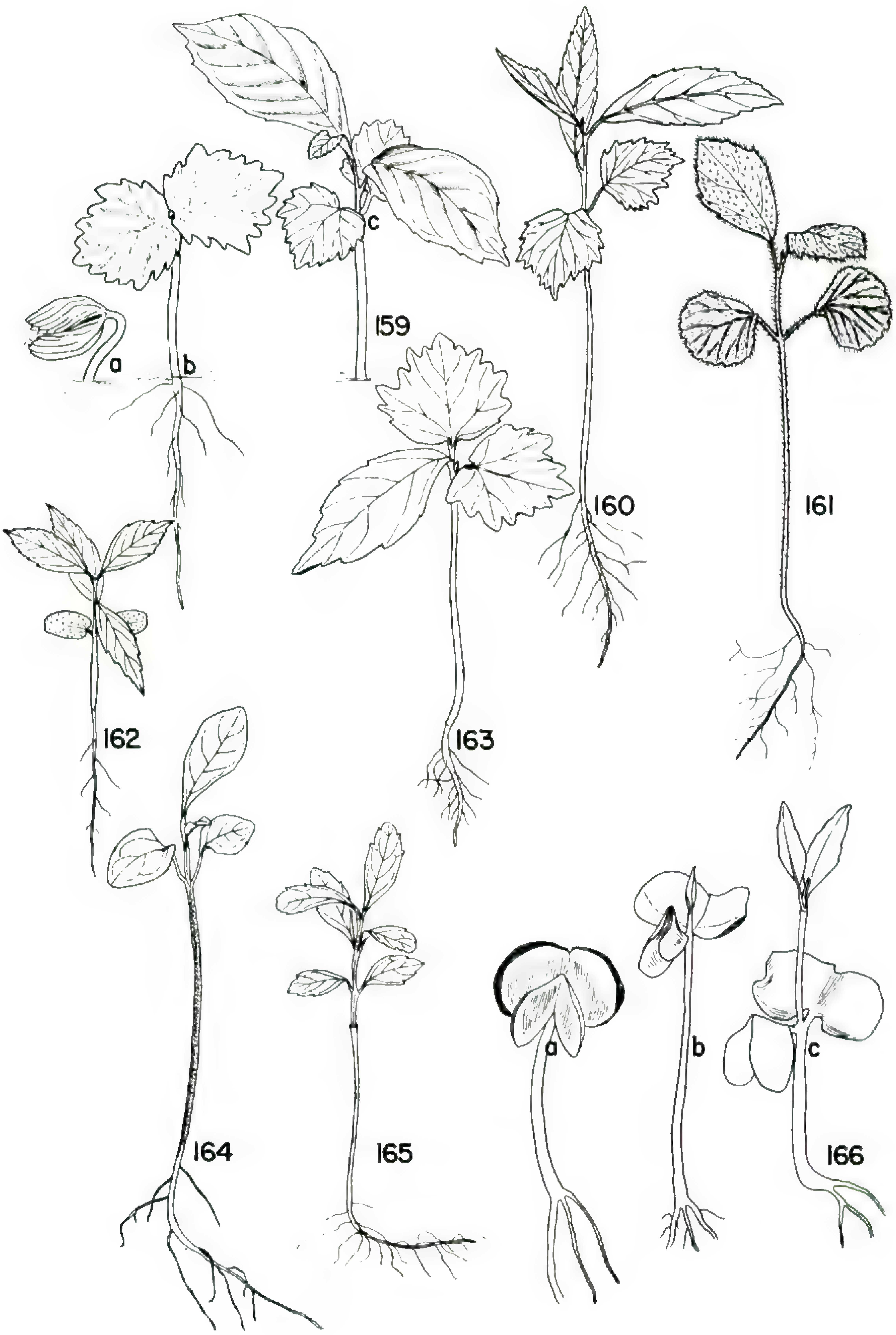

Plate 19

159. *Cordia nitida* (a & b × 1, c × ¾). 160. *Cordia sulcata* (× ¾). 161. *Cordia lima* (× 1). 162. *Tectona grandis* (× ½). 163. *Cordia borinquensis* (× ½). 164. *Cestrum macrophyllum* (× ½). 165. *Citharexylum fruticosum* (× ½). 166. *Avicennia germinans* (× ½).

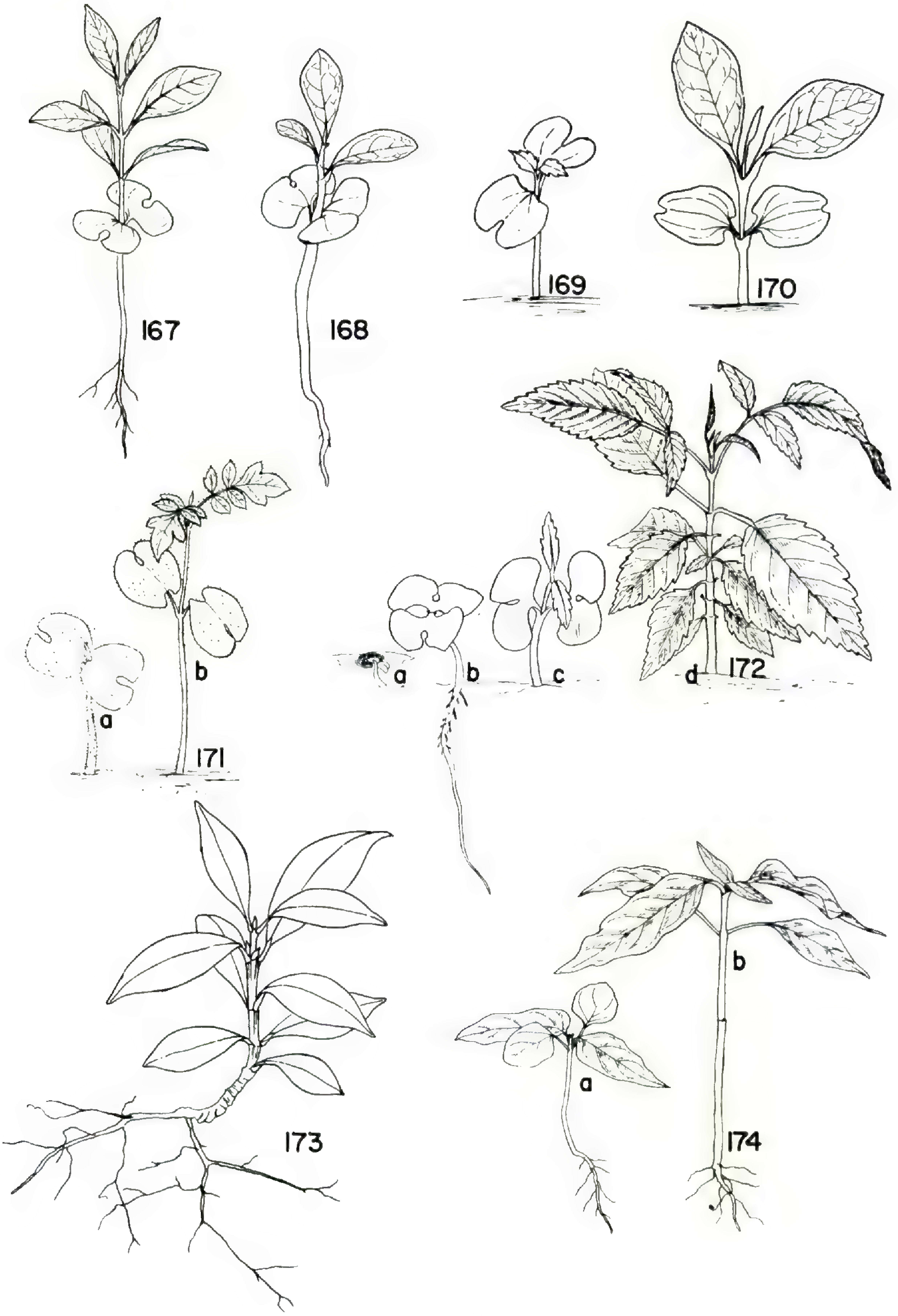

Plate 20

167. *Tabebuia heterophylla* (× ½). 168. *Tabebuia rigida* (× ½). 169. *Spathodea campanulata* (× ½). 170. *Crescentia cujete* (× ½). 171. *Jacaranda mimosifolia* (a & b × ¾). 172 *Tecoma stans* (a × ½, b & c × 1, d × ½). 173. *Hillia parasitica* (× ½). 174. *Psychotria berteriana* (a & b × ½).

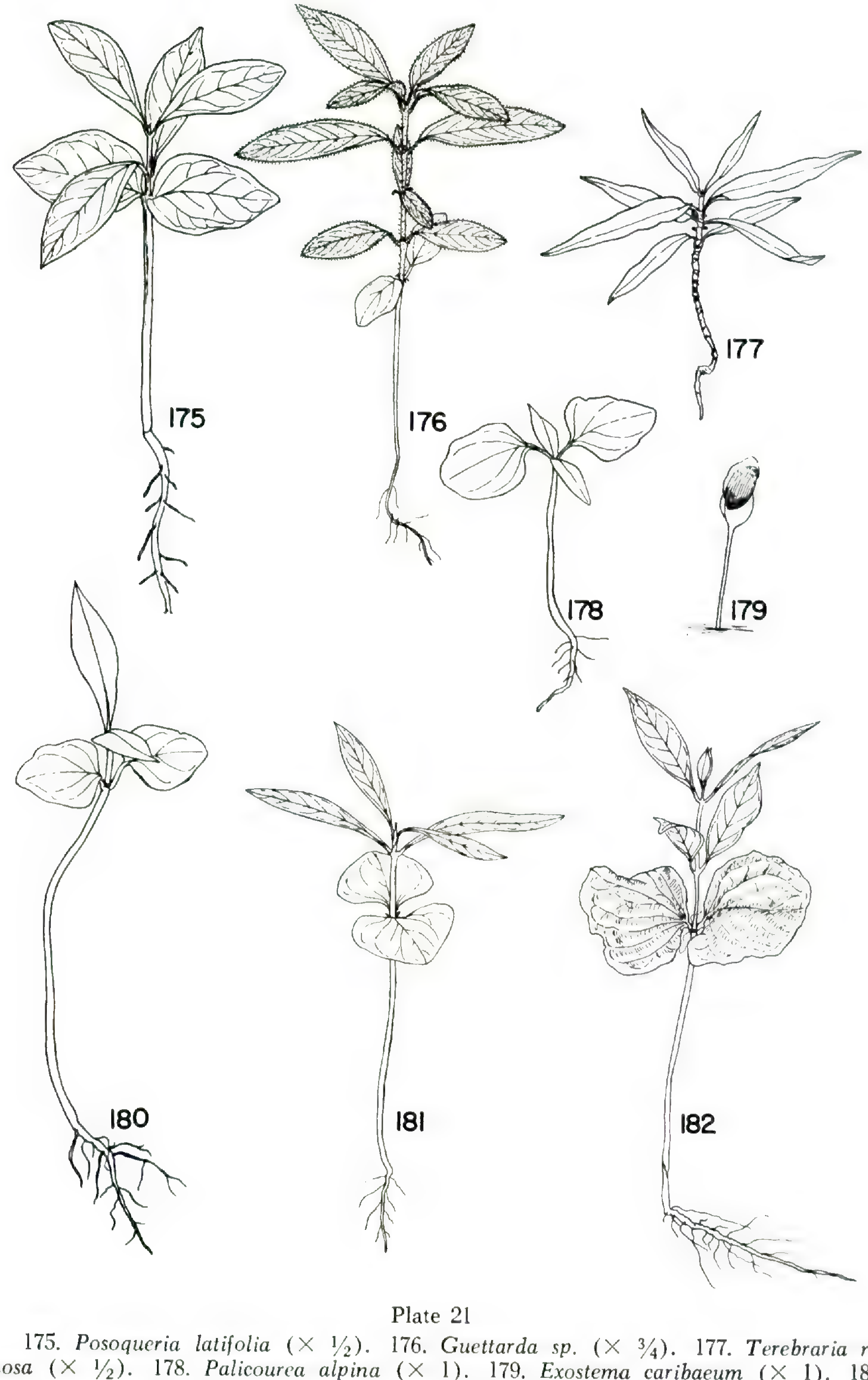

Plate 21

175. *Posoqueria latifolia* (× ½). 176. *Guettarda sp.* (× ¾). 177. *Terebraria resinosa* (× ½). 178. *Palicourea alpina* (× 1). 179. *Exostema caribaeum* (× 1). 180. *Genipa americana* (× ½). 181. *Ixora ferrea* (× ¾). 182. *Coffea arabica* (× ½).

NOTES ON THE LECYTHIDACEAE OF PANAMA

By John D. Dwyer

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In 1958 Woodson (in Woodson & Schery, Ann. Missouri Bot. Gard. **45:** 115-136. 1958) published a treatment of the *Lecythidaceae* for the Flora of Panama. This included six genera and approximately 14 species. As the genus *Couroupita* Aubl. is treated only cursorily, it is difficult to state categorically how many species Woodson considered to be present on the Isthmus. As less than 75 collections are cited for the six genera, with almost half of these collections being assigned to *Gustavia superba* (H.B.K.) Berg., it is obvious that additional collections of Panamanian *Lecythidaceae* are highly desirable. In commenting on the material of *Couroupita* available for examination, Woodson remarked (loc. cit., p. 127): "An adequate herbarium representation of *Couroupita* is one of the outstanding desiderata for a complete flora of Panama." As a result of the field work of Chambers, Duke, Dwyer, Ebinger, A. Robyns, Sexton, and Stern sporadically in Panama during the past seven years, some 34 new collections of the family are available for study, including three collections of *Couroupita,* all but five of these having been collected east of the Canal Zone, especially in the Province of Darien which borders Colombia.

The numerical arrangement of genera and species followed by Woodson will be adopted as far as is practical in this paper. All collections cited are deposited in the herbarium of the Missouri Botanical Garden. The citation "*Stern et al.*" refers to the collections of Stern, Chambers, Dwyer and Ebinger made in 1959.

1. Gustavia L.

1. *Gustavia nana* Pittier, Contr. U.S. Nat. Herb. **26:** 5, *pl. 2-4,* 1927; Woodson in Woodson & Schery, Ann. Missouri Bot. Gard. **45:** 120. 1958.

darien: Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 928;* Cativo Swamp, El Real, *Duke 4825;* Río Canelon, *Sexton 212;* sine sp loc, *Sexton 101 A.*

The fruit of *Duke 4825,* though immature, illustrates well the very broad opercular region characterizing *G. nana.*

2. *Gustavia superba* (H.B.K.) Berg, Linnaea **27:** 444. 1856.

canal zone: Madden Dam, *Dwyer & A. Robyns 13; Stern et al. 47.* darien: Río Canelon, *Sexton 256;* vic El Real, 1 mi down from Pinogana, *Stern et al. 112;* Paya & Pucro, *Stern et al. 406.* panama: Isla de Pedro Gonzales, *Dwyer 1690*; Isla Tabaguilla, *Duke 5887.*

I observed this species in full flower at Fort Sherman on the Atlantic side of the Canal Zone in April, although no collection was made. In July, 1962, Duke collected near Yaviza in the Province of Darien a fruiting specimen of *G. superba,* with lanceolate leaves, measuring up to 70 cm in length and 10 cm wide, and puberulent beneath. The foliage matches that of *Stern et al. 410* collected earlier at Paya in Darien. The immature fruit, measuring up to 7 cm in diameter, seems typical for

Ann. Missouri Bot. Gard. **52**(3): 351-363. 1965.

the species despite the fact that the surface is rougher and pustulate. As puberulent leaves have not been reported for *G. superba*, I am describing the new variety *puberula*.

Gustavia superba var. **puberula** Dwyer, var. nov.

A var typica foliis distincte infra puberulis differt.

DARIEN: below Yaviza, Río Chucunaque, *Duke 4881* (MO, holotype); Paya, Río Paya, *Stern et al. 410*.

2. Grias L.

1. *Grias pittieri* Kunth in Engl., Pflanzenreich **IV** 219 2 (Heft 105): 29. 1939; Woodson in Woodson & Schery, Ann. Missouri Bot. Gard. **45**: 122. 1958.—Fig. 1.

DARIEN: Comarça del Barú, Puerto Armuelles, between Cañazo & Cocos, *Stern & Chambers 141*.

The leaves of this collection appear to be consistently short-auriculate at the base. An Allen collection, *5216*, from the nearby Golfo Dulce area in Costa Rica,

Fig. 1. *Gustavia pittieri*. A. fruits: upper, internal view showing seeds, lower, external view, ca ×½; right, external view showing calycine ring, ca ×1. From *Stern et al. 410*.

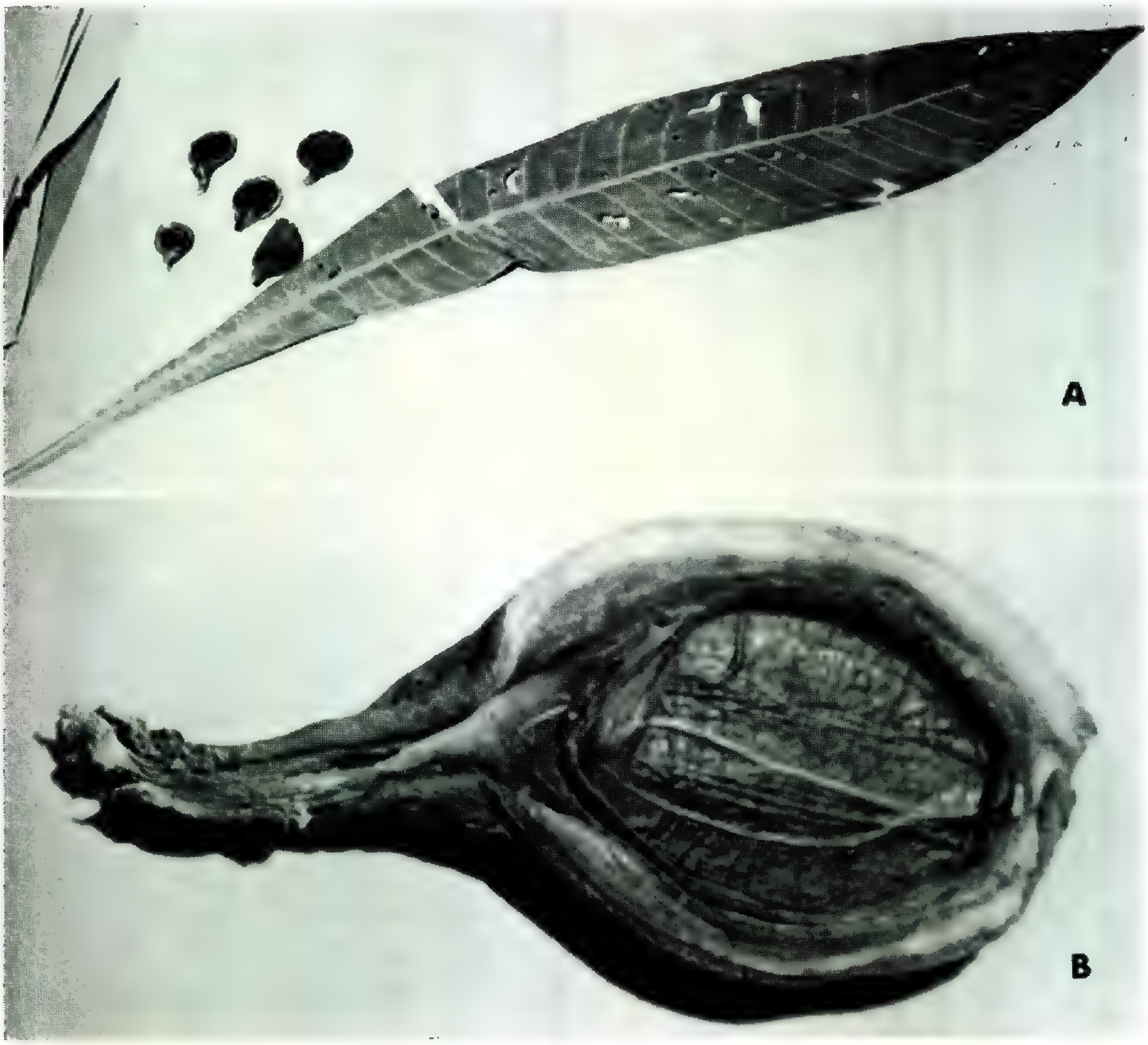

Fig. 2. *Grias dariensis* (holotype). A. leaf with fruit, ca $\times 1/8$; B. fruit, internal view, ca $\times 1 1/4$.

deposited in the herbarium of the Missouri Botanical Garden, shows the lamina with more obvious auricles.

2. *Grias* **dariensis** Dwyer, sp. nov.—Fig. 2.

Arbores parvae ad 11 m altae; folia lanceolata hic ad 65 cm longa, ad 12.5 cm lata, acutissima magne ad basim attenuata sessilia, costa supra ad apicem prominula, ad basim subplana latioreque venis secundariis prominulis $\pm$ 40 angulo 70° ascendentibus rectis ultime bifurcatis cir 5-10 mm proxime margines eis mediis 20-25 mm distantibus, lamina coriacea nitida glabra venis intermediis evanescentibus; fructus caulini diffusi obpyriformes vel oblongi, ad 3.5 cm longi, circ 2 cm lati, apice truncati annulo calycino apicale ad 3 mm alto margine tenue exocarpio in sicco paucis granulatis pustulis ornato brunneo vix ruguloso, pericarpio ad 1 mm lato semine fortasse solitario plano-convexo integre loculum complente, pedicello ad 10 mm longo, ad 7 mm lato, lignoso.

DARIEN: El Real, *Stern et al. 119* (MO, holotype)

The new species is, like *G. sternii,* distinguished from *G. fendleri* and *G. pittieri*

by its very acute lanceolate leaves. While its fruits fall in the same general size range of those of *G. pittieri,* they are slightly larger with the calycine ring more distinct and the pedicels considerably shorter.

3. *Grias* **sternii** Dwyer, sp. nov.

Arbores parvae ad 35 m altae; folia apice fascicularia lanceolata, ad 1 m longa, ad 13 cm lata, acutissima sessilia lamina magne atttenuata ad basim vix cordata, costa supra prominula sed proximaliter planiore prominente intra (ad basim praecipue) ad apicem evanescente venis secundariis ± 40 angulo 50° ascendentibus rectis eis mediis 15-22 mm distantibus ultime circ 5 mm proxime marginem bifurcatis sic undulatam venam submarginalem formantibus, lamina coriacea nitida glabra marginibus regularibus; flores non visi; fructus caulini diffusi oblongi, ad 5 cm longi, ad 3.3 cm lati, truncati certe biloculares (ovario prime quadriloculato) septo tenui, pericarpio ad 3.5 mm crasso coriaceo leviter rugoso in sicco brunneo minute crustuloso annulo calycino apicale circ 12 mm diametro vix prominulo. endocarpio chartaceo laeve subincarnato diversicolore gracile, pedicello ad 1.5 cm longo, 0.5 cm lato, coriaceo, seminibus hic oblongis, ad 3 cm longis, 1.2 cm latis, arillo ornatis.

DARIEN: El Real, Río Tuira, *Stern et al. 772* (MO, holotype).

The new species, named in honor of William Stern of the Smithsonian Institution, is readily distinguished from *G. fendleri* and *G. pittieri* by its very acute and lanceolate leaves. The fruits, noted in the field as "immature" are almost twice as elongate as those of *G. pittieri* and are borne on much longer pedicels. Unlike the newly described *G. dariensis, G. sternii* has a larger fruit with a much thicker wall and a vague opercular ring. Whether the fact that the fruits of *G. sternii* are crustulose while those of *G. dariensis* are pustulate is of any significance, additional collections will determine.

4. *Grias* **megacarpa** Dwyer, sp. nov.—Fig. 3.

Arbores ad 45 m altae; folia oblanceolata ad 32 cm longa, ad 11 cm lata, acuta ad basim cuneata, petiolis ad 4 cm longis, ad 0.2 cm latis supra planis infra convexis puberulis, costa supra prominente acutaque infra prominente venis secundariis ± 20 rectis angulo 45° ascendentibus ad margines curvantibus venis tertiis patentibus prominulis angulo recto secundariis venis dispositis, lamina chartacea supra glabra infra diffuse pubescente; flores non visi; fructus turgidi ovato-elliptici, ad 11 cm longi, ad 6 cm lati, ad apicem cuneati ultime obtusi basi obtusi, annulo calycino nullo vel fortasse paucis irregularibus sed uniseriatis punctis notato, eis circ. 1.5 cm apice distantibus, pariete pericarpii ad 1 mm crasso, pulpo in sicco rubro, semine solitario.

DARIEN: confluence of Río Chucunaque & Río Canclones, *Duke 5122* (MO, holotype).

I am placing this species in the genus *Grias* provisionally, although I feel that flowering collections will substantiate my suspicion that it is a new genus. The leaves are remarkably like those of the couroupitas, although the fruit of the new taxon is obviously not of the cannon-ball type so characteristic of *Couroupita.*

Fig. 3. *Grias megacarpa* (holotype). A. foliage and fruit, ×½; B. fruit, internal view showing single seed, ×2½.

The fruit, while possessing a pulp which not only dries like that of the grias but matches it histologically, is extraordinarily large for a *Grias* (compare Fig. 3 with Fig. 4) and lacks any distinct vestige of the calyx. The mimeographed field notes of Duke list *5122* as *Pouteria carpechiana* (H.B.K) Bachm. (*Sapotaceae*) and the fruit

Fig. 4. *Grias dukei* (holotype). A. foliage and fruits, ×¼; B. fruits: left, external view; right, internal view, ×1.7.

is described as edible. While the foliage of *P. carpechiana* bears a striking resemblance in form and texture (but not typically in size) to the new taxon, nevertheless the fruits are obviously different.

5. *Grias* **dukei** Dwyer, sp. nov.—Fig. 4.

Arbores ad 10 m altae; ramuli teretes; folia sessilia (maiora pseudopetiolata) apice ramulorum modeste crebra, 0.5-2 cm distantia, laminis maioribus hic oblanceolatis, ad 65 cm longis, ad 14 cm latis, minoribus distincte lanceolatis acutisque, costa supra plano-convexa ad 2 mm lata, prominente infra praecipue ad basim ca maiorum foliorum basaliter magne prominente in uteroque latere alam angustam ad 5 mm. latam ferente, venis secundariis principalibus ± 25 prominulis angulo 50° ascendentibus juxta marginem bifurcatis venis intermediis evanescentibus, limina rigido-chartacea concolore fortasse glabra marginibus parvorum foliorum leviter revolutis; fructus caulini oblongi, ad 5 cm longi, ad 2.5 cm lati, apice truncati cicatrice operculi plano circulare ad 1.5 cm lato, percarpio lignoso, circ 3.5 mm crasso, exteriore vix costato rugulosoque in sicco brunneo sub amplificatore minute farinoso, endocarpio subincarnato (ovario prime quadriloculato) septo tenuiore, pedicellis ad 0.5 cm longis, ad 0.25 cm latis; semina non vidi.

DARIEN: Río Pirre, 2-5 mi above El Real, *Duke 5090* (MO, holotype).

The oblanceolate shape of the larger leaves with their bases strongly attenuate as a slender wing on each side of the costa readily distinguishes *G. dukei*. The rela-

Fig. 5. *Couroupita idolica* (holotype): leaves, cauliflorous branches with buds, ×½.

tively large and thick-walled fruit (5 cm long and 0.35 cm thick [wall]) matches that of the newly described *G. sterni* but is borne on much shorter and more slender pedicels. The fruits of *G. dukei* are farinose on the surface which may prove to be of some significance when more material is available. The new species is named in honor of James Duke of the New Crops Research Center, USDA, Beltsville, Maryland.

3. COUROUPITA Aubl.

1. *Couroupita* **idolica** Dwyer, sp. nov.—Fig. 5.

Arbores magne ad 35 m altae; ramuli laeves glabri cicatricibus petiolorum plerumque depresso-globosis ad 5 mm. latis vix conspicuis; folia obovato-oblonga et parum inaequilateralia, ad 22 cm longa, ad 8.5 cm lata, apice obtusa curvataque basi cuneata, costa supra angustiore vix prominula, infra promimenter convexa venis secundariis ± 20 prominulis praecipue infra, angulo ascendentibus proxime margines bifurcatis ramulis arcuatis venis tertiis parum prominulis inconspicuis angulo recto venis secundariis dispositis, lamina chartacea hic in sicco subconcolore venis solum puberulis; flores 20-50 alternis in caulifloris ramulis, eis teretibus laevibus brunneis ad 25 cm longis, ad 7 mm latis, dispositi, pericellis ad 15 mm longis, crassis angularibus ascendentibus lignosis, aliquibus distantibus aliquibus geminis; flores lobis calycis sexibus oblongo-rotundis, ad 4 mm longis, ad 4 mm latis, in toto glabris crassis carnosisque; petala sexa fortasse inaequalia, 2.5-3 cm longa, 2-2.6 cm lata, concaviora; androphorum revolute cucullatum petaloideum, staminibus multis omnibus fertilibus, filamentis in inferiore parte inverse subulatis, 1.5-2 mm longis, apice 0.5 mm latis, antheris sessilibus circ 0.6 mm longis, circ 1 mm latis, connectivo nullo, filamentis mediorum staminium crassosubulatis, ad 3.5 mm. longis, apice ad 0.65 mm latis, antheris rotundis, ad 1 cm longis, circ 0.8 mm latis; filamentis distalibus in fasciculis 2-5 antheriferis; jugatis, ad 8 mm longis, pars ovarii supra calycem operculata, circ 3 mm longa, circ 7 mm lata, stylo nullo, stigmatibus jugatis cylindricisque ad 1 mm longis, ovulis multis in sexibus loculis dispositis; fructus non visi.

VERAGUAS: Río Trinidad, Río de Jesuś, *Dwyer 1311* (MO, holotype), *Restrepo s.n.* (MO).

In July 1961 I rode by horse from the village of Río de Jesús (Veraguas) to the Río Trinidad to collect material of the famous idol tree. I had learned of this tree from the padres of the church at Santiago (Prov Veraguas). After an hour and a half ride the guide pointed to a tree of about 100 feet, majestically dominating a patch of mesophytic forest. The most striking feature of the tree was not the short cauliflorous branches with withered flowers within reach of the machete but the fact that the shadowy base of the goliath was enclosed in a sheet metal fence. On a platform surrounding the foot of the tree stood a crucifix before which some plastic flowers had been placed. To this tree natives came from far and wide to worship during Easter Week. The crucifix, however, stood not as a memorial to this worship but rather as a stern warning against the rituals which were reputed to terminate in a bacchanalia.

For the flowers described above I wish to express my thanks to Prof. Roberto Restrepo of the Normal School in Santiago, Panama.

On the basis that Seeman collected the type of *Couroupita odoratissima* "in the forests of Río de Jesús, between Santiago and Puero Mutis, Veraguas" one might expect that my taxon belongs here. However, Pittier, as Woodson points out (loc. cit., p. 127), "distinguishes *C. odoratissima* Seem. as a "low spreading savanna tree, branched almost from the base" . . . yet Seemann assigns a height of 60-80 feet to the type trees of *C. odoratissima*."

The two principal reasons for describing the material as a new species is that the flowers here are much larger than those reported for *C. odoratissima* and secondly that the distal filaments of the stamens are mostly fused into flat band-like antheriferous fasicles which appear in outline like the body of a foliose lichen. As far as I know this has not been reported for any Panamanian species of *Couroupita*.

The flowers of the new species are reddish in color. The common names for *C. idolica* are: "El Arbol de Granadillo" and "El Granadille de Las Huacas."

2. *Couroupita* **magnifica** Dwyer, sp. nov.

Arbore magnae ad 60 m altae; ramuli laeves in sicco longitudinaliter marcescentes glabri cicatricibus petiolorum oblongis vel subrotundis as 5 mm latis notati; folia conspicue alterns satis distantia obovato-lanceolata, ad 20 cm longa, ad 8.0 cm lata, apice obtusa rare breviore latioreque acumine, basi attenuato-cuneata, lamina angustam alam in uteroque latere petiolorum formante, costa supra proximaliter prominula acutaque distaliter angustiore, infra prominente, venis secundariis principalibus $\pm$ 20 rectis angulo 45° ascendentibus ultime arcuatis bifurcatisque proxime margines, saepe mediam venam subparallelem inter jugum venarum ferentibus, venis tertiis supra vix conspicuis infra prominulis recto angulo venis secundariis dispositis, lamna subcoriacea glabra praeter basim venarum secundariarum; pedicelli 1-2 cm longi, supra plani infra subconvexi, ad 3.5 mm lati; flores hic circ 20 alterni in caulifloris ramulis dispositi, lobis calycis sexibus subrotundis, ad 6 mm longis, circ 6 mm lats, crassis carnosisque pracipue proximaliter glabris praeter margines minuto ciliatos exteriore rugis minutis ornatis; petala sexa suborbicularia, ad 12 mm longa, circ 10 mm lata, crassa laevia glabra praeter margines minute ciliolatos; androphorum reflexo-cucullatum carnosum staminibus fortasse omnibus fertilibus crebrerrimis, filamentis staminium proximalium linearicylindricis, ad 2 mm longis, connectivo gracili circ 0.75 mm longo, antheris oblongo-rotundis circ 0.35 mm longis, filamentis staminium distalium liberis crassioribus brevioribusque, connectivo nullo; ovarium (hic fructus juvenilis?) turbinatum, circ 10 mm longum, ad 10 mm latum, pariete pericarpii circ 2 mm crasso quadriloculatum, exteriore verrucis circularibus vel substellatis, 0.7-1 mm latis ornato, endocarpio in sicco cyaneo, ovulis multis in placentis axillaribus affixis.

DARIEN: vic of Campamente Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 930* (MO, holotype)

As the petals, persistent in the very young fruit, tend to remain closed, measur-

ing here about 12 mm in length, we can make a calculated guess that the flowers of the new species measure about 3 cm in diameter at anthesis. Thus the flowers of *C. magnifica* approximate those of *C. parviflora* Standley from Bocas del Toro, although Woodson (loc. cit., p. 127) observed tha ". . . the flowers of the type specimen of *C. parviflora* obviously are not fully expanded. . . ." The new species is distinguished from *C. parviflora* by its alate petioles bearing blades which are occasionally acuminate at the apex. The sepals of *C. magnifica* are glabrous except marginally, and the petals unlike those of *C. parviflora* are ciliolate marginally and the anthers here measure only 0.35 mm in length.

4. Lecythis Loefl.

1. *Lecythis tuyrana* Pittier. Contr. U. S. Nat. Herb. **26:** 9, *pl.* 7. 1927, Woodson in Woodson & Schery, Ann. Missouri Bot. Gard. **45:** 128, *fig. 40.* 1958.—Fig. 6, C, D.

DARIEN: vic of El Real, Río Tuira, foothills of Cerro Pirre, Don Pablo Othón's pasture, *Stern et al. 738*; vic of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 883.*

The collection 738 is from a small tree 30 feet high, 8 inches in diameter with yellow flowers, while 883 is from a tree 150 feet high, 3 feet in diameter. The fruits collected from both trees (cf. Fig. 6) match well the one in Pittier's paper (loc. cit.) as well as the sketch in Woodson's paper (loc. cit.).

2. *Lecythis* **elata** Dwyer, sp. nov.—Fig. 6A, B.

Arbores ad 60 m altae; folia ut in *L. tuyrana* oblonga, ad 33 cm longa, ad 11.5 cm lata, abrupte acuminata basi obtusa brevi-auriculataque venis secundariis principalibus 20-30 rectis angulo 80° ascendentibus, lamina coriacea glabra, petiolis 0.5-1 cm longis, flores non visi; fructus urceolati, 7.5-9.0 cm longi (sine operculo), 10-11 cm lati, loculo 5.5-7.5 cm alto, zona calycina submedia saepe obliqua prominente plutoidea, 3-5 mm lata non erosa, zona infracalycina plus quam superiore contracta, zone supracalycina 3-5 cm longa, gradatim convexa vel rare subrecta labio convexo, ± 10 mm lato, parvis verrucis vel dentibus munito, exteriore lignoso brunneo sublaeve vel multis irregularibus magnisque tumoribus notato, ore pyxidii 5-7 cm in diametro, operculo ad 2.5 cm longo, ad 11 cm in diametro, margine late crenulato concavioreque, parte superiore magnis irregularibus radialibus verrucosis vel foveatis tumoribus notata, umbone prominente ad 1.2 cm longo, ad 2.5 cm in diametro, intus vacuo, parte inferiore lamellis radialibus prominentibus lignosis vel sulcis angustis altisque ornati; semina non vidi.

DARIEN: vic of Campamento Buena Vista, Río Chucanaque above confluence with Río Tuquesa, *Stern et al. 876* (MO, holotype)

The six fruits of *L. elata* available for study (Fig. 6A) are considerably smaller than are those of *L. tuyrana* Pittier (Fig. 6D) as well as being smoother and less contracted in the zone below the calycine ring. The shelf-like ring is not erose and the supracalycine zone is usually more concave than in Pittier's species. In addition the operculum is much more tumorous on the outer surface with a strikingly prominent umbo, hollow within and in general suggesting a thimble, and an

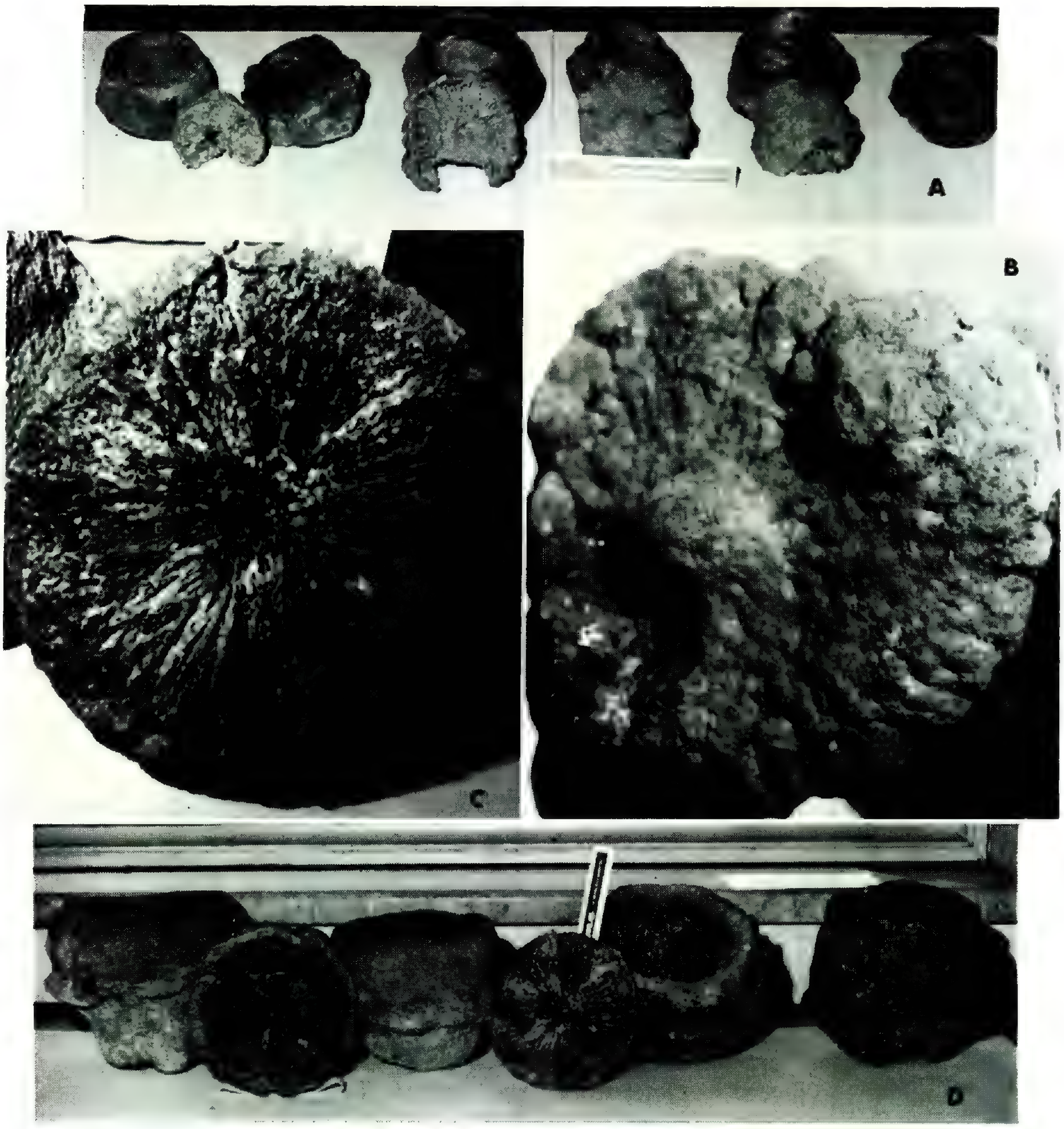

Fig. 6. *Lecythis elata* (holotype). A. fruits with several opercula, ×⅛; B. operculum of fruit, upper surface, ×¾. *Lecythis tuyrana*. C. operculum of fruit, lower side, ca ×½; D. fruits with several opercula, ×⅛.

edge which is markedly concave. *L. tuyrana* has a much flatter and smoother operculum with its edge fitting flush against the rim of the pyx. A glance at Mier's plate (loc. cit., *pl. 43*) is sufficient to show that the pyx of *L. ampla* Miers, known from the Province of San Blas, Panama (and from Colombia), is much larger than that of *L. elata* and *L. tuyrana*.

3. *Lecythis ampla* Miers, Trans. Linn. Soc. **30:** 204, *pl. 43, figs. 1-2.* 1874; Woodson in Woodson & Schery, Ann. Missouri Bot. Gard. **45:** 128. 1958.

DARIEN: Punta Guayabo Chiquita, 14 mi N of Colombia, *Stern & Chambers 163.*

This sterile collection is supported by a wood sample (Yale Wood no. 51655). Two common names are listed on the label "coco" and "salero."

Fig. 7. *Eschweilera pittieri*. A. foliage and fruit, ca ×1; B. fruit, lateral view showing operculum and calycine ring, ca ×¼. From *Duke 5222*.

5. Eschweilera Mart.

1. *Eschweilera panamensis* Pittier, Contr. U.S. Nat. Herb. **26:** 12. 1927; Woodson in Woodson & Schery, Ann. Missouri Bot. Gard. **45:** 130. 1958.

darien: Río Chico, nr Boca de Tesca, *Duke 5222*.

This is the second collection of the species, the type *(Pittier 4394)* having been collected on the Atlantic slope at Puerto Obaldia, Prov San Blas.

2. *Eschweilera pittieri* Kunth in Engl., Pflanzenreich **IV** 219 2 (Heft 105): 93. 1939. Woodson in Woodson & Schery, Ann. Missouri Bot. Gard. **45:** 131, *fig. 41*. 1958—Fig. 7.

darien: Río Tucuti, Tucuti, *Duke 5254;* Ensenada Guayabo, between Punta Guayabo Grande & Punta Guayabo Chiquita, *Stern & Chambers 176*.

The fruit of the Duke collection is a perfect match for the one sketched in Woodson's paper (loc. cit., p. 132, *fig. 41*). The Stern & Chamber's collection has much larger flowers than Woodson noted for the species, measuring up to 7 cm in diameter. Stern & Chambers note that their collection is from a tree 17 inches in diameter with creamy yellow flowers; two common names "huasca" and "tuave" are listed; a wood sample was taken (Yale Wood no. *51667*).

3. *Eschweilera calyculata* Pittier, Contr. U.S. Nat. Herb. **12:** 97, *pls. 1-2*. 1908; Woodson in Woodson & Schery, Ann. Missouri Bot. Gard. **45:** 133. 1958.

canal zone: Galena Point, *Dwyer & Robyns 158*.

Unfortunately there was no fruit on the tree which we collected in April, 1965. The tree, about 35 feet high, had striking cream-orange buds.

4. *Eschweilera* **woodsoniana** Dwyer, sp. nov.—Fig. 8.

Arbores parvae (?) ramulis teretibus laevibus glabris; folia 1-2 cm distantia, laminis oblongis, 8-10.5 cm longis, 4-5 cm latis, abrupte breviacuminatis basi ob-

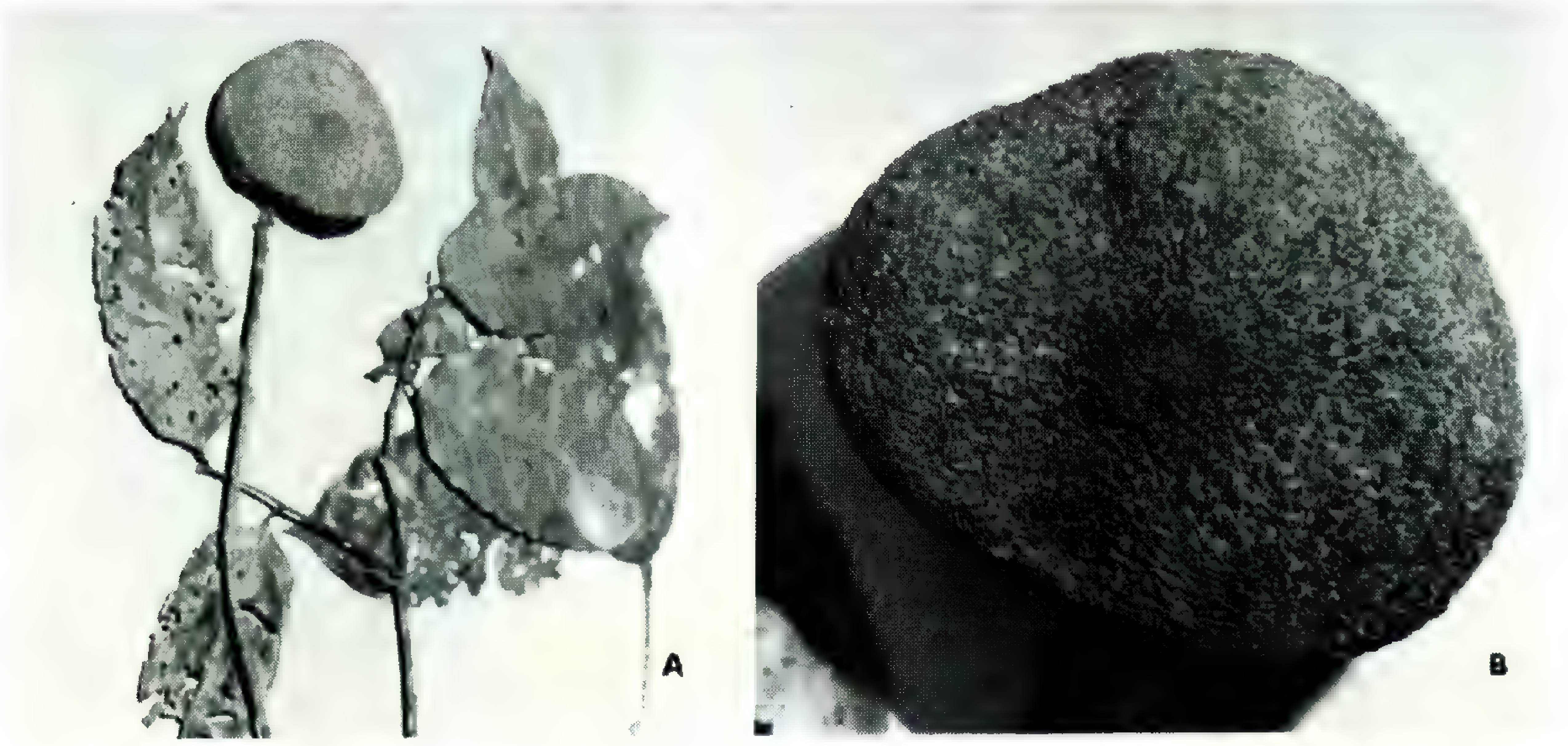

Fig. 8. *Eschweilera woodsoniana* (holotype). A. foliage and fruit, ×¼; B. fruits, opercular view, ×1.

tusis, costa supra prominula infra vix prominente venis secundariis ± 10 prominulis arcuatis supra evanescentibus prominulis infra prominulis eis mediis 1-1.5 cm distantibus venis intermediis sub amplificatore recticulis, lamina nitida glabra subcoriacea, petiolis teretibus coriaceis, ad 6 mm longis, ad 1.5 mm latis, glabris; flores non visi; fructus biloculati depresso-globosi, ad 2.5 cm longi, ad 5.5 cm lati, annulo calycino circ 5 mm ab basi fortiter contracto convexoque cincti, lobis annuli calycini sexibus vix ad 1 mm prominentibus, zona supracalycina 1-1.5 cm longa, operculo vix convexo umbone vix prominente ad 2 mm alto, 0.4-2 cm in diametro, margine acuto strato exteriore marginis saepe paullum retracto ad 0.8 cm et undulato, exocarpio in sicco brunneo minute ruguloso vix asperoque, endocarpio laeve tenui nitido brunneo, septo chartaceo angusto eccentrico, seminibus 6, subtriangularibus vel hemisphericis, ad 2.5 cm longis, 1.4-2.0 cm latis, ad 0.8 cm altis, arillo laeve tenui dimidium obtecto, endocarpio prominulis radialibus interseminalibus lineis ornato.

DARIEN: wooded ridge S of El Real, *Duke 5062* (MO, holotype).

The new species, named in honor of Dr. Robert E. Woodson, is readily distinguished from the other Panamanian species by possessing a pyx which is more than twice as broad as long and is subsessile with the pedicel attachment obviously eccentric.

5. *Eschweilera* sp.

The following collection *(Duke 6124)* has only flowers. The description of these is as follows: sepala sexa oblonga circ 3 mm longa, 2-3 mm lata, carnosa fortasse glabra; petala sexa libera praeter basim aliqua staminifera basi, oblonga, 1.5-2 cm longa, 1.3-1.6 mm lata; androphorum involuto-cucullatum parte proximale multis fertilibus staminibus obtecta, antheris sessilibus bis plus longitudine filamentis apice dilatis; ovarium biloculatum stigmatibus solitariis circ 3 mm longis, 1.3 mm latis, glabris.

DARIEN: locality unknown, *Duke 6124.*

SPECIES CROSSES IN HELIANTHUS: III. DELIMITATION OF "SECTIONS"[1]

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The genus *Helianthus* comprises 108 species, according to Watson (1929), although only about 70 would be recognized in a more conservative treatment. Asa Gray (1884) subdivided the genus into "annuals" and "perennials." It is perhaps significant that he failed to give Latin designations to his sections. Watson (1929) resorted to purely artificial groupings, the Rubri, in which the lobes of the disk corollas are red or purple, and the Flavi, in which the lobes are yellowish. The artificiality of this treatment is apparent when it is realized that several species are known in which both colors of disk corollas occur. However, it is true that the red and brown colors are common in the annuals and rather rare in the perennials. Rydberg (1932) in his treatment of 27 species for central North America set up six subdivisions, the annuals and five groups of perennials. Thus it is apparent that a completely satisfactory subgeneric classification, other than the recognition of annuals and perennials, has never been achieved for the genus.

In the first paper of this series (Heiser, Martin & Smith, 1962) it was pointed out that the genus comprised three more or less distinct groups: (1) North American annuals including the tap-rooted perennials, (2) North American herbaceous perennials, mostly from rhizomes, and (3) South American, more or less shrubby perennials. Although not all possible crosses have been attempted between the various species of the genus, a large number has now been made and a general picture of relationships, based on the results of hybridization, is beginning to emerge. It is now possible to divide the North American perennials group into two "sections": the "Divaricati," mostly confined to eastern and central North America, with the exception of *H. californicus* and *H. nuttallii*, and the "Ciliari," mostly limited to the southwestern United States and northern Mexico. Although for the most part the species of the two groups are well set off morphologically, as yet no completely satisfactory morphological characters have been found on which to base formal subgeneric classification. Additional study may reveal such characters, but it is entirely possible that none exist. It seems probable, nevertheless, that the four "sections," (1) the annuals and tap-rooted perennials, (2) the "Divaricati," (3) the "Ciliari," and (4) the South American perennials, form four distinct phylogenetic lines.

The present paper summarizes the results of artificial hybridizations not previously reported as well as certain other evidence bearing on the relationships of species. For descriptions of most of the species, reference may be made to Watson (1929). Herbarium specimens of the hybrids described here as well as their parental

[1] This work was aided by a grant from the National Science Foundation. I would like to express my appreciation to my assistants, Mr. Alvin Reeves and Mr. Willard Yates.
Ann. Missouri Bot. Gard. **52**(3): 364-370. 1965.

species, giving details as to source, are deposited in the herbarium of Indiana University. Table 1 gives a summary of the new hybrids and these will be discussed according to the headings listed therein.

"Annuals"

Hybrids between the species of the group are, with a few exceptions, readily secured and generally show highly reduced pollen and seed fertility. One of the most significant exceptions involves *H. agrestis* which thus far has not produced seeds in crosses with other annuals. Another kind of exception is seen with *H. tephrodes* (Heiser, 1955). This species is difficult to grow at Bloomington but a few hybrids have now been secured with *H. canus.* The high fertility of the hybrids and the fact that *H. tephrodes* is very similar to *H. canus* suggest that perhaps they had better be regarded as members of one species. The only hybrid secured in crosses of *H. tephrodes* with the apparently closely related *H. niveus* died as a seedling. Hybrids also have not been secured between *H. canus* and *H. niveus,* although they share many morphological features and both cross readily with *H. debilis* ssp. *debilis.*

The majority of the new hybrids involves *H. paradoxus,* a species recently described (Heiser, 1958) and earlier thought possibly to be extinct. Since the original description was based on a single specimen, several taxonomists (oral communications) questioned whether it was a "good" species. Therefore, I made a trip to the type area in 1961. Although I did not find the species at the type locality (7 miles west of Fort Stockton, Texas), I did find one population of about 50 plants ten miles north of Ft. Stockton *(Heiser 4779).* The plants were growing in a moist, roadside meadow beside a stream, confirming the suspicion that this was more or less a paludose species. No other populations were found in spite of detailed search, although *H. annuus* was found to be extremely common in the area. It now seems probable that the natural hybrids of *H. paradoxus* previously reported (Heiser, 1958) probably involve *H. annuus* as the other parent rather than *H. neglectus.*

The plants were not yet in seed; but through the courtesy of Mr. Noel M. Hall, Jr., a local high school teacher, a large number of achenes were sent to me later in the year. Some of these were grown the following year at Bloomington and some at Urbana, Illinois, by Dr. Dale Smith. All 25 plants grown at Bloomington resembled the parent plants, but Dr. Smith reported that some of his plants were obviously hybrids with *H. annuus.* The plants collected in nature and those grown from seed fit the original description fairly well except that vigorous individuals may have a few prominent teeth in the lower part of the leaf margin and the stems are somewhat more harshly pubescent than those of the type. The chromosome number was determined as $n = 17$.

Reciprocal crosses of *H. paradoxus* with the annuals *H. agrestis, H. canus, H. niveus,* and the two perennials failed; but an abundance of seed was secured in crosses with five annual taxa. Those hybrids which were successfully grown all showed the highly reduced pollen stainability (Table 1) characteristic of the other

annual hybrids. Seed set varied from 0-20% in these hybrids upon open pollination, and controlled sister crosses gave no seed. The results of the hybridization and the fact that this species is quite distinct morphologically indicate that it is clearly entitled to the rank of species in spite of its apparently very restricted distribution.

"Perennials: Divaricati"

All of the new hybrids in this group involve diploid species except the last (6347) which is between hexaploids. Three of the artificial hybrids now reported (6248, 6370, and 6371) confirm previously suspected natural or spontaneous garden hybrids (Heiser, Martin & Smith, 1962). The new hybrids are similar to those previously reported in this group in that few hybrid seeds are usually secured, but the hybrids show moderate to high fertility and exhibit a high number of bivalents at meiosis.

The hexaploid hybrid is of some interest since it marks the first successful cross with *H. californicus*. The species failed to give seeds in crosses to the hexaploids, *H. strumosus* and *H. tuberosus*, and several diploids. However, that *H. californicus* belongs to this group of perennials is supported by its morphology since it is very similar to certain forms of the diploid species, *H. nuttallii*, which readily crosses to other eastern perennial diploids. Although the hybrids of *H. resinosus* × *californicus* give very high pollen stainabilities (Table 1), seed set of sister crosses was low, ranging from 5 to 15%. The F_1 hybrids morphologically appear to be nearer *H. resinosus* than *H. californicus*. An F_2 generation, however, gave some segregates showing features of *H. californicus*. It is thus clear that the F_1's are true hybrids rather than selfs.

"Perennials: Ciliari"

A group of species, *H. arizonicus*, *H. ciliaris*, *H. dissectifolius* and *H. laciniatus*, recently treated by Jackson (1963), morphologically form a very distinct group; and crosses of species within this group (*H. arizonicus* × *laciniatus* and *H. laciniatus* × *dissectifolius*) give rather fertile hybrids with a regular meiosis. To this group may be added *H. pumilus* of Colorado and Wyoming and *H. gracilentus* of southern California and northern Baja California, both diploids. Although morphologically somewhat removed from the remainder of the species of the group, these two species fit more nearly into this "section" than into any other. It is significant that hybrids of these have been secured in crosses to each other and with typical members of the group (*A. gracilentus* × *laciniatus* and *H. pumilus* × *laciniatus*, Table 1).

Helianthus cusickii, a diploid perennial of the northwestern United States, poses a somewhat special problem. Morphologically it is one of the most "extreme" species in the genus and does not clearly fit into any of the "sections." This species grows poorly at Bloomington and only a few crosses have been attempted with it. Crosses failed with three annual species and three eastern perennials but three weak plants were secured from a cross with *H. pumilus*.

That the perennials of this group are strongly isolated from the remainder of the genus is indicated by the crosses thus far attempted. Both the tetraploid and

hexaploid races of *H. ciliaris* have failed in crosses with three eastern tetraploid and three hexaploid perennials (Heiser & Smith, 1964). *Helianthus laciniatus* and *H. pumilus* have both failed to cross with three annuals and three eastern diploid perennials. Crosses have, however, been secured of *H. niveus* × *pumilus* and *H. niveus* × *laciniatus,* the former giving nearly sterile hybrids and the latter giving plants which died as seedlings (Table 1).

Annuals × Perennials

Although efforts have continued to secure additional hybrids between annuals and perennials using new strains of species previously tested, there are few new ones to report. Most of those that have been secured involve *H. niveus,* a species of Baja California; and it appears that this is the one species that bridges the North American groups as far as crosses are concerned. Hybrids of this species have also been secured with *Viguiera porteri* (Heiser, 1963). It is worth noting that Blake (1918) considered *H. niveus* as one of the two species intermediate betweeen *Helianthus* and *Viguiera.* In view of the hybridization results and that this species may be transitional to *Viguiera,* it is tempting to suggest that it is a "primitive" species which may be the nearest approach among living species to the original ancestral stock of *Helianthus.* Although placed with the annual group, it is a tap-rooted perennial; and such a species could have served as the progenitor of both the strict annuals and the perennials from rhizomes as was postulated by Babcock (1950) for *Crepis.*

The second new annual × perennial hybrid is *H. agrestis* × *floridanus.* The annual *H. agrestis* of Florida has failed to give seeds in crosses attempted with eight annual species and eight perennial species. There is some question regarding the taxonomic identity of the perennial parent (*Godfrey 62629*) although it is clearly closely related to *H. floridanus* and *H. angustifolius.* The hybrids secured were extremely weak and had malformed leaves and unusually small heads, and the flowers failed to produce anthers. Backcrosses attempted with the parental species as the male parents failed to produce seed. The failure of *H. agrestis* to cross with the other annuals raises some question about its placement in this "section." On morphological grounds it does not appear particularly closely related to the other annuals with the possible exception of *H. paradoxus* and at the same time it does not appear to be closely related to any perennial species.

In view of the fact that many of the annual × perennial hybrids have fairly good chromosome pairing, the statement made in the first paper of this series that there has been considerable differention in the chromosomes of the two groups requires some modification. However, the fact remains that all of the hybrids thus far secured are highly sterile which suggests that either genic or cryptic structural hybridity may be involved.

Hybrids of *H. annuus* with the perennials "*H. lactiflorus, H. maximiliani, H. rigidus,* and *H. scaberimus*" have recently been reported by Georgieva-Todorova (1960, 1962, 1963). Hybrids of both *H. rigidus* and *H.* × *laetiflorus* are not unexpected with *H. annuus,* since both of them are closely related to *H. tuberosus* which

is known to hybridize with *H. annuus.* It is difficult, however, to accept identifications of some of the perennials he has listed. His "*H. rigidus*" from the photograph given appears more nearly like *H. grosseserratus.* What he means by "*H. scaberimus*" since he cites no authority is uncertain. *Helianthus scaberrimus* Benth. is a synonym of *H. Bolanderi,* and *H. scaberrimus* Ell. is a synonym of H. *laetiflorus* (Watson, 1929). He gives no photograph of *H. maximiliani* but the "hybrids" insofar as can be determined from the photograph show no influence of that species. Furthermore, I cannot accept his suggestion that *H. maximiliani* and *H. annuus* are not very different genetically.

Pigment Analysis

In 1915 Cockerell found that the ligules of certain species of *Helianthus* when immersed in a KOH solution turned red to varying degrees whereas the ligules of other species showed no change. We have extended his observations to include all of the species which we have used in the crossing program reported in this series of papers except for *H. radula* which produces reduced ligules or lacks them entirely. For the most part at least three geographical samples have been tested for each species, and we have found that herbarium specimens give the same reaction as does living material although the intensity may vary to a degree. All members of the "western" and "eastern perennials" showed a positive reaction from moderate to strong, with the exception of *H. angustifolius* and *H. mollis,* which gave no reaction. Nine of the "annuals," on the other hand, gave negative results, while four species were positive. Of these last four, two, *H. anomalus* and *H. deserticola,* gave moderately strong reactions, whereas the other two, *H. agrestis* and *H. paradoxus,* gave very weak reactions. Thus, the reaction of KOH, probably indicative of a chalcone pigment, does not coincide exactly with the groups which have been set up as a result of hybridization and morphological studies.

Summary

Four "sections" may be recognized in *Helianthus*: (1) the annuals and taprooted perennials, (2) the "Divaricati," perennials primarily of central and eastern North America, (3) the "Ciliari," perennials, primarily southwestern North America, and (4) South American, more or less shrubby perennials. The "sections" are based primarily on the results of hybridization and it is thought that they may represent four different phylogenetic lines. Twenty-nine new artificial hybrid combinations are reported. Of particular interest among these are hybrids involving the recently described *H. paradoxus.* The results of the hybridizations along with morphological considerations indicate that this taxon justifies specific rank. Also of interest are the hybrids, *H. agrestis* × *floridanus* and *H. californicus* × *resinosus,* since they represent the first successful crosses involving *H. agrestis* and *H. californicus.* The possibility that *H. niveus* is "primitive" species is discussed. Reactions of ray flowers when treated with KOH do not give results that coincide with the "sections" as delimited above.

Table 1. New Artificial Interspecific Hybrids in *Helianthus*.

Accession Number	*Species*[1]	*Number of Plants*[2]	*Pollen Stainability Percentage*[3]	*Meiosis: Number of Bivalents*[4]
A. "Annuals"				
6041	argophyllus × neglectus	1	10	
6048	canus × tephrodes	4	99	
6318a	canus × debilis	3	25	15–17
6318b	debilis × canus	3	18	
6319a	debilis ssp. debilis × niveus	2	34, 88	(15–)17
6207	niveus × debilis ssp. debilis	4	64	15–17
	F_2 of above	4	86	
6320	niveus × debilis ssp. runyonii	2	5	15–17
6409	niveus × tephrodes	1; seedling died		
6325b	paradoxus × annuus (St. Louis)	7	8	9–11
6325c	paradoxus × annuus (Texas)	3	12	
6324b	paradoxus × argophyllus	4	6	13–14
6327b	paradoxus × debilis ssp. debilis	6	25	13–15
6328a	debilis ssp. runyonii × paradoxus	6	4	13
6328b	paradoxus × debilis ssp. runyonii	6	5	
6330	paradoxus × petiolaris	7	14	13
B. "Perennials: Divaricati"				
H579A	atrorubens × carnosus	2	49	
6414	atrorubens × floridanus	5	76	16–17
6248	decapetalus (2*n*) × carnosus	1	33	
H580B	heterophyllus × atrorubens	4	71	15–17
6371	longifolius × mollis	3	43	17
6371	maximiliani × decapetalus (2*n*)	7	84	17
6370	microcephalus × giganteus	6	55–97	17
H593B	mollis × decapetalus (2*n*)	3	82	17
6347	resinosus × californicus	5	98	quadrivalents present
C. "Perennials: Ciliari"				
6340a	arizonicus × laciniatus	4	91	17
H473a	cusickii × pumilus	3	30	17
H603a	gracilentus × pumilus	5	28	15–17
H603b	pumilus × gracilentus	1	15	
H585a	laciniatus × dissectifolius	3	79	
H585b	dissectifolius × laciniatus	6	93[5]	17
H586a	laciniatus × gracilentus	2	35, 63	
H586b	gracilentus × laciniatus	2	65, 85	13–15
H589	pumilus × laciniatus	1; seedling died		
D. Annuals × Perennials (including those mentioned in earlier papers*)				
*6199	canus × angustifolius	8	10	few pairs
*WM2014	debilis × floridanus	2	5	4–17
*H651B	debilis ssp. hirtus × occidentalis	2	4	?–17
6415	floridanus × agrestis	10	no pollen	
NIVJI	niveus × laciniatus	2; seedlings died		
*6374	niveus × microcephalus	6	10	14–17
*6211	niveus × nuttallii	2 (weak)	10	14–17
*6375	niveus × occidentalis	15	9	15–17
H644A	niveus × pumilus	1	13	13–17

[1] Female parent given first. Although all hybrids were made reciprocally, frequently only seeds from one combination germinated.

[2] In some cases a larger number of hybrids were secured in the annuals but only the number given was used for pollen counts.

[3] Mean given except in cases when there was considerable variability.

[4] Number of pairs observed in approximately 25 cells examined of one hybrid; where less than 17 pairs were observed the remainder of the chromosomes were associated in one or more chains or appeared as univalents.

[5] One plant showed 10%; the other five averaged 93%.

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ON THE SYSTEMATIC POSITION OF ALZATEA VERTICILLATA R. & P.

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In 1953 whilst I was working in Washington my late colleague and friend, Mr. Noel Y. Sandwith of Kew, drew my attention to a specimen of Klug's from Peru, which was very difficult to place in any known family. Sandwith thought it might belong in *Lythraceae.*

To my surprise the same gathering was found in the incertae sedis of most American herbaria and in Stockholm, whilst other specimens of the plant were placed under *Celastraceae, Rhamnaceae, Guttiferae,* and others.

Independently we identified the plant with *Alzatea verticillata* R. & P. and a collection so named from Bolivia was also found.

However, the systematic position was uncertain and my interest was whetted particularly during a survey of the literature covering the genus *Alzatea.* The problem has hitherto not been solved and this very interesting plant, a tree up to 14 m high from the Amazonian region, still remains without a satisfactory home in any family of the present taxonomic systems.

A historical review of the different attempts at classification is as follows:

Ruiz & Pavón described the genus *Alzatea* in 1794 under *Pentandria Monogynia* and in 1802 the species *A. verticillata,* between *Cervantesia* and *Myoschilos.*

The description of the seeds was drawn up by the authors but remained unpublished until 1954 (Fl. Per. Chil. **4,** ed. E. A. López). The habitat of the tree, figured in the manuscript of the Journal of H. Ruiz, was published in English by Dahlgren in 1946 and by Jaramillo-Arango in Spanish in 1952.

De Candolle in 1824 placed the genus in the *Celastraceae.*

Blume in 1826 when describing *Crypteronia* stated its affinity to be with *Alzatea* "Genus *Alzatea* Ruiz et Pavón valde propinquum."

In 1842 Walpers relegated this genus to *Genera dubia.*

Planchon, 1845, who knew this genus only from the description and plate of Ruiz & Pavón, discussed its affinities and suggested that it should be placed in the *Lythraceae.*

Bentham & Hooker, 1862, following perhaps De Candolle kept the genus within the *Celastraceae.* However, I do not think that this opinion carries any weight since they quoted "ex Ruiz et Pavón" and added "Genus nobis ignotus."

The first detailed description after the original one and its discussion is that of Miers in 1872 where he does agree that the plant is not a member of the *Celastraceae* or of the *Hippocrateaceae* but he suggests that together with *Crypteronia* the two could constitute a tribe (*Crypteronieae*) within the *Rhamnaceae.* This idea was supported especially by the position of the stamens.

Ann. Missour Bot. Gard. **52**(3): 371-378. 1965.

In 1911 Hallier reconsidered the question and came to the conclusion that the genus should be placed in the *Lythraceae*. This idea was taken up by Pilger & Kraus (Nachträge, 1915) although Koehne has not followed suit.

Hallier for a second time in 1918, reviewed the problem and suggested the family *Melastomataceae*.

Loesener, the monographer of the *Celastraceae*, quoting Miers, in 1942, eliminated the genus from this family and proposed to include it in the *Rhamnaceae* together with *Crypteronia* and *Tetrataxis* as a tribe of the subgroup *Crypteronieae*.

Subsequently, Macbride (Flora of Peru, 1951) retains *Alzatea* in the *Rhamnaceae* although he suggests affinity with the *Icacinaceae* on some characters and with *Guttiferae* by the leaves.

All these suggestions have tended more towards the rejection of *Alzatea* from the different families than in a search for its proper place. Therefore it was not keyed out in any family and it is not even mentioned in the several editions of the *Syllabus* (1908, 1912, 1924, 1936, 1964)! Its aberrant characters, particularly the parietal placentation have made impossible the naming of any specimen of *A. verticillata*.

Differences and Affinities

1. *Floral and vegetative characters.*

I shall briefly consider the most outstanding differences with the families cited below:

From *Celastraceae*, aestivation, number of ovules, position of the stamens; from *Rhamnaceae*, aestivation, number of ovules (erect), stipules, insertion of petals and stamens; from *Melastomataceae*, leaves alternate, corolla hypogynous, stamens, fruits, etc.; from *Guttiferae*, aestivation, stamens and disk, sepals, etc.

It approaches the *Rhamnaceae* by the aestivation, the parietal placentation and the stamens alternating with the calyx-lobes.

From the *Lythraceae*, the genus *Alzatea* differs only in the placentation (see discussion below). All the other characters are found in the different genera of that family: quadrate section of the branchlets, decussate leaves, inflorescences common to the ligneous genera, consistancy subcoriaceous leaves (*Galpinia, Lafoensia*), leaf-venation (*Lafoensia*), perianth 5-6-merous, very frequently found, and its coriaceous consistancy (*Ginoria, Galpinia*, etc.), absence of corolla, stamens homomerous, alternate with the calyx-lobes (*Galpinia, Tetrataxis, Crypteronia*, etc.), anthers with large connective, although they are very peculiar in *Alzatea*, capsular fruit 2-carpelar with two placentae each with two longitundial series of ovules, dehiscence loculicidal.[1]

The placentation of the *Lythraceae* has been recorded as either axillary or central which corresponds in fact to the same type. The ovaries are composed of

[1] The ovary and the fruit have been described as 2-carpelate and 2-locular, but the ovary is in fact 2-carpelate and 1-locular. When the fruit developes, a false septum grows between each pair of placentae towards the centre of the cavity and the capsule thus appears to be 2-locular.

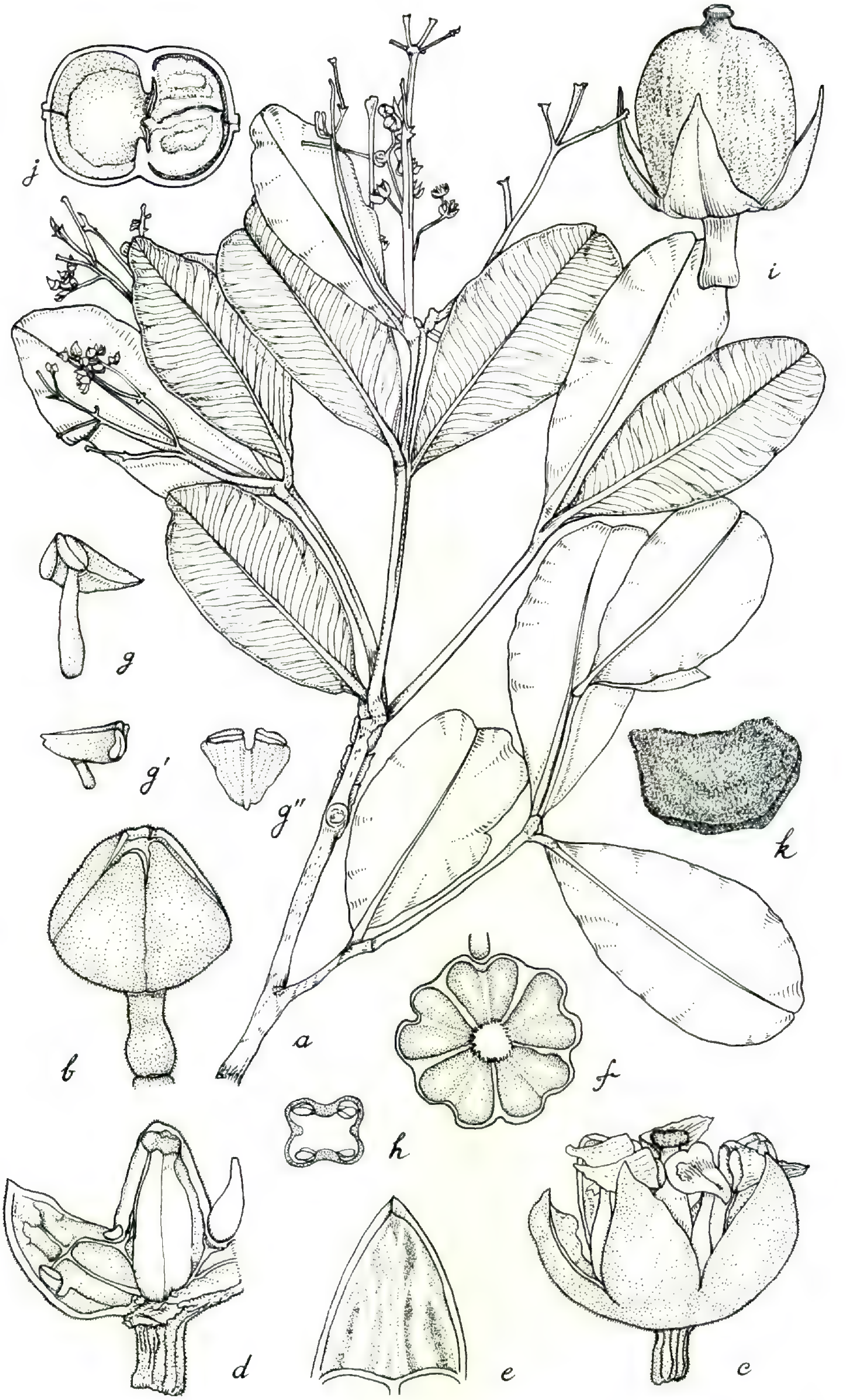

Fig. 1. *Alzatea verticillata.* a, twig ×½; b, bud ×5; c, flower ×5; d, part of flower, interior ×5; e, interior of a tepal ×7.5; f, disk ×5; g,g',g'', stamens ×5; h, transversal section of the ovary ×7.5; i, fruit ×4; j, transversal section of the same ×4; k, seed ×8. a-h- from *Klug 3349*, S; i-k from *Woykowski 6196*, P. A. Lourteig del.

completely separate locules or the septae are interrupted above the placentae; the number of the ovules is very variable, sometimes very high.

However, the placentation of some genera does not correspond always to the classical definition. The ovary is 1-locular in *Cuphea* with a central free placenta, dorsiventral, with a very characteristic dehiscence. In *Pleurophora* the ovary is 2-locular with a thick central placenta but one of the locules is narrower, sometimes very reduced and sterile (*P. anomala*) and the fruit is not dehiscent. *Diplusodon* shows a 2-locular ovary with a basal placenta bifid and these parts are adnate to the walls of the ovary; they are multiovulate. *Ammannia* subgen. *Cryptotheca* with one species, *A. microcarpa* (a herbaceous plant), occurs in Java, Timor and Celebes, and curiously shows a 1-locular ovary with a parietal placenta (cf. Koehne, Pflreich.).

After all these considerations and a study of Puri's paper, 1952, where he explains the variations and the evolution of the placentation in angiosperms, I have come to the conclusion that the placentation of *Alzatea*, the only character which has prevented botanists from including it in *Lythraceae*, is no bar to such inclusion in view of the other positively "lythraceous characters." To reinforce my conclusions I have had the aid of an anatomist and a palynologist as given below.

2. *Anatomical characters.*[2]

a) *Leaf*: *Lamina*. Dorsiventral. Hairs absent. *Epidermis* with thick cuticle. *Stomata* confined to abaxial surface, ranunculaceous. *Hypodermis* present on either side of the midrib. *Mesophyll* with 2-3 layers of palisade, including large mucilaginous cells. Thick-walled sclereids and large thick walled irregular cells, possibly secretory, frequent in spongy tissue. *Vascular* bundles bicollateral. Midrib with 2 wide, shallow vascular bundles facing each other and 2 small lateral vascular bundles, all with intraxylary phloem, forming an incomplete ring of vascular tissue. Each vascular bundle surrounded by thick-walled fibres. *Crystals* frequent, clustered. Tannin or similar substances frequent in palisade and mesophyll lining abaxial surface. *Petiole*. Elliptical in outline with one face flattened. *Ground tissue*. Outer zone of thick-walled lignitied cells. Inner tissue parenchymatous, irregular. Large thick-walled sclereids and secretory sacs frequent. *Vascular bundles*. A large central concentric bicollateral vascular bundle enclosing pith zone. 2-3 small lateral accessory vascular bundles, approximately concentric with intraxylary phloem. *Crystals*. Large clusters very frequent in phloem and also present in ground tissue. (Material from Peru, *Woytkowski 6169*).

b) *Stem*: *Cork* arising in pericycle; many-layered. *Endodermis* present. Numerous large radially flattened sclereids present in pericycle/secondary phloem. *Phloem* including concentrically arranged crystal cells and sclereids. Phloem and *xylem* in form of continuous cylinder traversed by narrow rays. *Intraxilary phloem* sometimes disintegrated, but evidence of its presence. Pith solid with numerous thick-walled sclerosed cells. *Crystals*. Clusters frequent in phloem. *Wood. Vessels*

[2] Contributed by Dr. Margaret Y. Stant of the Jodrell Laboratory, Kew Gardens, England.

small, solitary in multiples of 2-3. *Perforations* simple. Intervascular pitting medium, vestured. Pits to rays and parenchyma large and simple. *Parenchyma* scanty. *Rays* uniseriate, occasionally partially biseriate, about 2-12 cells high, heterogeneous. Fibres with simple pits, septate. (Materal from Bolivia, *Bang 890.*)

The following characters all of which are mentioned in the description above, appear to indicate that *Alzatea* is closely allied to the *Lythraceae.* Intraxylary phloem, bicollateral vascular bundles. Presence of mucilaginous cells, sclereids and other secretory elements. Pericyclic cork. Vessel pitting. Ray with. Septate fibres. Crystal type and distribution.

3. *Palynological characters.*[3]

Pollen isopolar, subtriangular, slightly depressed on the axis of the mesocolpium, dimorphic, longiaxial or subaequiaxial in meridional diameter, elliptic to subtriangular. P = 21-16μ, E = 16μ. Pollen tricolporate, ectoaperture elongate narrower towards the equator, endoaperture little visible. Not heterocolporate. Exine finely reticulate not striate, about 1μ. (Material from Peru, *Klug 3349.*)

This pollen recalls that of *Physocalymna* within the *Lythraceae.*

According to Dr. van Campo the pollen resembles that of *Physocalymna* (see Cos-Campos) a monospecific genus; its species (*P. scaberrimun* Pohl) occurs in the Amazonian region and in the Matto Grosso. It is also a big tree but its flowers are very showy with big coloured petals.

Conclusion

My research into the affinities of the genus *Alzatea* leads me to believe that the true position of this genus is in the *Lythraceae.* I base this conclusion on the following facts. (1) The floral and vegetative characters are not at variance with those in other genera in the family. (2) The anatomical features of the leaf and stem correspond to similar features found in the *Lythraceae.* (3) The palynological evidence also supports the above views.

Following Koehne's key (Pflreich.) this genus should be placed in the tribe of the *Lythreae* Koehne subtribe II. *Diplusodontinae* Koehne emend. Lourt.:

Subtr. II. *Diplusodontinae*

Semina a dorso compressa circumcirca ala cincta vel spongiosa (quae in *Alzatea*). Fructus maturi placenta maxima depressa, basalis vel placentatione parietali et ovulis 4-serialibus. Flores semper actinomorphi. Aothera dorso affixae.

I. Flores 6-5-meri. Calyx persistens .... Series I.

. . . .

. . . .

γ. Dissepimenta ovarii nulla. In fructo spurium septum inter placentis. Capsula loculicide 2-valvis. Flores homoeomorphi .... 10a. *Alzatea.*

Alzatea R. & P.

Ruiz & Pavón, Prodr. 40, *pl.* 7. 1784. Hedwig, Gen. 175. 1806. Roemer & Schultes, Syst. 569. 1819. Candolle, Prodr. **2:** 10. 1825. Sprengel, Syst. **1:** 826. 1825. Blume, Bijdr.

[3] Contributed by Dr. Madeleine van Campo of the Palynological laboratory of the Muséum, Paris.

17: 1154. 1826. Reichenbach, Consp. 208. 1828; Handbuch 301. 1837. Don, Gen Syst. **2:** 11. 1832. Lindley, Veg. Kingd. 588. 1833. Spach, Vég. Phan. **2:** 404. 1834. Endlicher, Gen. 1090. 1836; Enchir. 575. 1841. Meissner, Gen. 68. 1837. Heynhold, Nom. 42. 1841. Planchon, London J. Bot. **4:** 476-7. 1845. Bentham & Hooker, Gen. **1**(1): 359; 362-3. 1862. Miers. Tr. Linn. Soc. London **28:** 328-9. 1872, Pfeiffer, Nom. **1**(1): 129. 1873. Engler, Pflien. Nachtr. **2-3:** 202. 1908. Hallier, Med. Rijks. Herb. Leiden 1910: 29-32. 1911; Ibid. **35:** 17-18. 1918; Ibid. **41:** 7, nota 2. 1921. Pilger & Krause, Pflien. Nachtr. **4:** 188. 1915. Loesener, Pflien. ed. 1. **3**(5): 221. 1896; ed. 2. **20b:** 196. 1942. Weberbauer, Pflweit. **12:** 310. 1911; Andes per. 642. 1945. Macbride, Field Mus. Chicago **13**(3a, 1): 259, 392-3. 1951. *Alzalia* Dietrich, Vollst, Lex. Gärtn. **1:** 299-300. 1802. *Azaltea* Walpers, Rep. **1:** 539. 1842, ex errore! *Alziniana* Dietr. ex Pfeiffer, Nom. **1:** 129. 1873, in synonym!

Alzatea verticillata R. & P.

Ruiz & Pavón, Fl. Per. Chil. **3:** 20, *pl. 241.* 1802; **4:** 123. 1954; Field Mus. Chicago **21:** 204. 1940; Rel. hist. 322. 1952. Heynhold, l.c. 42. Rusby, Mem. Torr. Bot. Club **4:** 205. 1875. Macbride, l. c. 393.

Alzalia mexicana Dietrich, l. c. 299, nomen!

Material seen—Peru. Amazonas, Cerro de Escalero, alt 1300 m, Baum 3-6 m, Bl. gründlichweiss, *Ule 6750,* II 1903, K; Pitabamba, Santa Ana, alt 7-8000 ft, tree 30-40 ft, *Pearce s.n.,* XI 1866, K; San Marín, Zepelacio, nr Moyobamba, alt 1100-1200 m, forest, *Klug 3349,* X-XI 1933, GH, K, MO, S; Río Negro in the forest, alt 1000 m, tree 12 m high, *Woytkowski 6196,* 15 I 1961, MO, P. Bolivia. *Bang 829,* K, NY, US.

Appendix

I should also recall that *Crypteronia* has all the characters of the *Lythraceae.* The only difference is the polygamous dioecious inflorescence, which has not been found in the family But I have described a genus for Madagascar, *Capuronia,* a small tree or shrub that is dioecious. Moreover, the anatomy (Metcalfe & Clark) is that of the *Lythraceae.* I believe that its right place is that assigned by Bentham & Hooker, that of the *Lythraceae.*

Acknowledgments

I should like to thank the following scientists who have helped me: Dr. Stant of Kew, and Dr. van Campo of Paris for their contributions to the anatomy and palynology respectively; the authorities of Missouri Botanical Garden for providing herbarium materials; my friend Dr. N. L. Bor for kindly reading the manuscript. Finally, I must record my indebtedness to N. Y. Sandwith of Kew, whose scholarship and intimate knowledge of botany in general and that of South America in particular, has been of the greatest value to me in my studies. His recent tragic death at a comparatively early age is a deplorable loss to all students of South American botany and not least to me personally.

Résumé.

Sur la position systématique de Alzatea verticillata R. & P.—Le genre monospécifique *Alzatea* a été décrit par Ruiz et Pavón parmi le *Pentandria Monogynia.* De Candolle fut le premier à le placer dans une famille. *Celastrineae Tribus II Evonymeae;* il fut suivi par presque tous les botanistes (Reichenbach, Don, Spach, Lindley, etc.), même si dans certains cas le genre était placé parmi les *Genera dubia,* ou genres *incertae sedis.* Sprengel l'a placé dans les *Rhamneae.* Blume et Planchon ont trouvé des rapports avec les *Lythracées* et, ce dernier a suggeré de le placer dans cette famille. Mais, les arguments ne furent jamais très convaincants et malgré les diverses temptatives, ce genre s'est vu réjeté des *Celastracées, Rhamnacées, Lythracées, Hippocrateacées, Guttifères,* sans qu'il puisse être classé dans aucune famille.

Il s'agit néanmoins d'un arbre de la forêt amazonienne qui a été récolté plusieurs fois. Bien que la constitution florale et les caractères végétatifs permettaient de placer cette plante parmi les *Lythracées,* la placentation pariétale s'y opposait et ce caractère a constitué la barrière à laquelle les botanistes se sont heurtés.

Heureusement les études modernes sur la placentation et son évolution ont démontré d'une part qu'il n'existe pas une rigidité aussi absolue entre les différents types de placenta-

tion et d'autre part, que, puisque dans l'évolution on peut passer d'un type à l'autre, ce caractère ne doit pas avoir la priorité dans la classification. (Actuellement, plusieurs familles comprennent des genres ayant des types de placentation différents).

Après les observations des caractères systématiques, végétatifs, floraux, de l'anatomie et du pollen, l'auteur arrive à la conclusion qu'il n'y a pas de raison valable qui s'oppose à l'inclusion du genre *Alzatea* dans les *Lythracées*. Il trouverait sa place dans la Tribu des *Lythreae* Koehne Subtribus *Diplusodontineae* Koehne emend. Lourt.

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NEW DISCOVERIES OF GNETUM IN TROPICAL AMERICA

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As yet the peculiar gymnospermous genus *Gnetum* in the New World is only known by six species in the Amazon Basin and in the Guyana Highland. These species are differently distributed: 1) *G. urens* (Aubl.) Bl. follows the coastal rain forest from the lower Orinoco River (Catalina) to south of the lower Amazon River (Bragança); 2) *G. nodiflorum* Brongn. inhabits savannahs and wood edges in the Guyana Highland from its eastern border up to the Rio Negro in Venezuela, and similar situations of the Terra Firme in the Amazon region; 3) *G. paniculatum* Spruce is rarer in the Guyana Highland and runs from its eastern border to its southern border, following the Rio Negro valley; 4) *G. venosum* Spruce is found only in the rain forest of the lower and middle Amazon River up to Manáos; 5) *G. Schwackeanum* Taub. has a similar distribution, but seems to extend a little farther up the right tributaries (Rio Madeira, Rio Acre); 6) *G. Leyboldii* Tul. is bound to the wet rain forests, even swampy igapó forest, in the real lowlands along the whole Amazon River, stopping at the tributaries below the rapids (cachoeiras).

By the kindness of several American herbaria specimens of this genus came under my eyes, collected in Panama, and thus extending considerably the area of the genus. Of course now the question arises, where their affinities are to be sought. Morphologically, they stand forth by large, often almost orbicular leaves shining silk-like on the upper surface by means of a dense subepidermal layer of fibres parallel to the secondary nerves. Inflorescences, flowers and fruits correspond to those of *G. Leyboldii* Tul.; now this species is Amazonian. But the large geographical gap is bridged over by a discovery made by Oscar Haught[1] in 1935 in the valley of Rio Magdalena in western Colombia. This sample agrees completely with those from Panama.

In the meantime, Swedish botanists, E. Asplund and F. Fagerlind with G. Wibom, have discovered the genus *Gnetum* even in Ecuador[2] and R. E. Schultes with G. A. Black and J. Cabrera also in southwestern Colombia. They found two species, *G. nodiflorum* Brongn. and *G. Leyboldii* Tul. In Ecuador the species reach the district of Tunguragua, in Colombia that of Rio Uaupès. On the eastern slope of the Andes, they ascend a little higher up together with the rain forest (to about 250 m above sea level); as maximum altitude Asplund fixed 1200 m on Rio Pastaza. Both species however stop at the lower part of that eastern slope. The taxon of the Rio Magdalena remains separated by the Eastern Cordillera. By this segregation its morphological differentiation from the similar Amazonian *G. Leyboldii* may well

[1] His samples were named by Killip as *Gnetum colombianum* on the herbarium sheets, but this name seems to have never been published.

[2] An old-mentioned species of Ecuador, *Gnetum trinerve* Spruce (Notes of a botanist in the Amazon and Andes **2** (1908) 279)), according to its type specimen at Kew has proved to be a *Loranthacea* described by Trelease as the type of his *Phoradendron trisulcatum* (Trelease, the genus *Phoradendron* (1916) 155).

Ann. Missouri Bot. Gard. **52**(3): 379-386. 1965.

be understood. As the Magdalena Basin had its last regression of the sea only in Pliocene times,[3] and thus became accessible for a land Flora not earlier, even the age of differentiation of its taxon from the similar *G. Leyboldii* in the Amazon Basin is made probable. On the other side, between the Magdalena Valley and Panama, since that time there were no mountain obstacles for its distribution. One may expect that the same taxon will be found in the interlying region too.

Its taxonomic position seems nearest to *G. Leyboldii* Tul. The characters of flower and fruit agree so well that it is distinguished only by the shape and fibrousness of the leaves and by the shorter and poorer inflorescences. Thus it is introduced here with the rank of a variety below *G. Leyboldii.*

In order to show it in the whole relationship and to include, at the same time, the other above mentioned discoveries, it may be welcome to have established a conspectus[4] of all the American species of that genus.

A. Bract collars of inflorescences close to each other (in male ones at the most 2 mm, in female ones at the most 10 mm distant), their margin slightly incurved, their base tapering sinuously into the axis.

- I. Adult leaves large, up to 20 × 15 cm, heavily coriaceous, generally not becoming black when dry. Whole inflorescence much ramified, loose, partial inflorescence on a stalk about 10 mm in length, male one about 15 mm, female about 30 mm long. Male bract collars in anthesis 2 mm distant, female ones 4-8 mm distant, in fruit about 10 mm distant. Sterile female flowers of male inflorescence obovate, fertile female flowers ellipsoidal, acuminate. Fruit oblong, parallel-edged, 45-50 mm long, 20 mm wide, fleshy, its outermost layer thick (1 mm when dry), the innermost solid. .... *G. Leyboldii* Tul.
  - a) Leaves broad-elliptic (length to width 1.4-1.7), gleaming silky by means of dense fibres under the epidermis. Inflorescence bearing only 1-2 whorls at the main axis. Colombia to Panama. .... var. *Woodsonianum* Mgf.
  - b) Leaves elliptic (length to width 1.7-2), without dense fibres. Inflorescence bearing 3-4 whorls at the main axis. Amazon basin. .... var. *Leyboldii.*
- II. Adult leaves large, up to 17 × 8 cm, somewhat more tender, often becoming black when dry. Whole inflorescence much ramified, condensed, partial inflorescence almost sessile, about 10 mm long. Male bract collars close to each other even in anthesis, female ones up to 2 mm distant. Sterile female flowers of male inflorescence shortly ellipsoidal, blunt. Fertile female flowers almost globose. Fruit broad-ellipsoidal, 50 mm long, 30 mm wide, its outermost layer very thick (3 mm when dry), the innermost solid. Guyana highland till Rio Negro. ..*G. paniculatum* Spruce
- III. Adult leaves small, up to 12 × 6 cm, softly coriaceous, yellowish green, gleaming silky by means of dense subepidermal fibres. Whole inflorescence loose, but its lateral twigs mostly not again ramified; partial inflorescence shortly stalked, male one about 10 mm, female one about 20 mm long. Male bract collars 1 mm distant, female ones up to 10 mm distant. Sterile female flowers of male inflorescence cylindric, fertile female flowers oblong, acuminate. Fruit ellipsoidal, slightly obovate, 35-40 mm long, 18-20 mm wide, its outermost layer thin, fibrous, the innermost chartaceous. Coastal forest from Orinoco to Amazon river. ....*G. urens* (Aubl.) Bl.

B. Bract collars of inflorescences distant (in anthesis 10-20 mm, in fruit mostly 20 mm), dish-like, their margin upright, their base not tapering into the axis.

- I. Adult leaves up to 18 × 9 cm, heavily coriaceous, not gleaming, generally not becoming black when dry. Whole inflorescence very loose, partial inflorescence on a stalk about 20 mm in length, about 100 mm long. Male bract collars in anthesis

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[3] Buergl, Historia Geologica de Colombia, in Revista de la Academia Colombiana de Ciencias Exactas, Fisicas y Naturales **11** (1961) 173, 170, *fig. 40.*—Gerth, Der Geologische Bau der Südamerikanischen Kordillere (Berlin 1955) 157, 240.

[4] Completing that of a monograph in Bull. Jard. Bot. Buitenzorg, 3 sér., **10** (1930) 498.

10 mm distant, female ones 20 mm, fruiting 20 mm. Sterile female flowers of male inflorescence ovate, acuminate; fertile female flowers ellipsoidal. Fruit shortly ellipsoidal, 30-35 mm long, 20 mm wide, its outermost layer thin ($\frac{1}{4}$ mm when dry), the innermost very thin. Guyana Highland and Amazon region. .... *G. nodiflorum* Brongn.

II. Adult leaves up to 12 × 6 cm, softly coriaceous, becoming slightly black when dry, slightly gleaming silky by means of parallel subepidermal fibres. Whole inflorescence loose, but only moderately ramified; partial inflorescence on a stalk 10-15 mm in length, 30-50 mm long. Bract collars in anthesis 10-15 mm distant. Sterile female flowers of male inflorescence obovate; fertile female flowers ellipsoidal, acuminate. Fruit oblong-obovate, 35 mm long, 20 mm wide, its outermost layer thin, almost without fibres, the innermost chartaceous. Lower and middle Amazon river. .... *G. Schwackeanum* Taub.

III. Adult leaves up to 13 × 6 cm, softly coriaceous, often obovate, becoming black when dry, gleaming silky by means of dense subepidermal fibres. Whole inflorescence rather loose; partial inflorescence on a stalk 10-15 mm in length, 50-60 mm long. Bract collars in anthesis 5 mm distant. Sterile female flowers of male inflorescence oblong-obovate; fertile female flowers oblong, acuminate. Fruit ellipsoidal, 7 cm long, 4 cm wide, ellipsoidal with acuminate top, its outermost layer fleshy and fibrous, 3 mm thick, the innermost chartaceous. Lower and middle Amazon river. .... *G. venosum* Spruce.

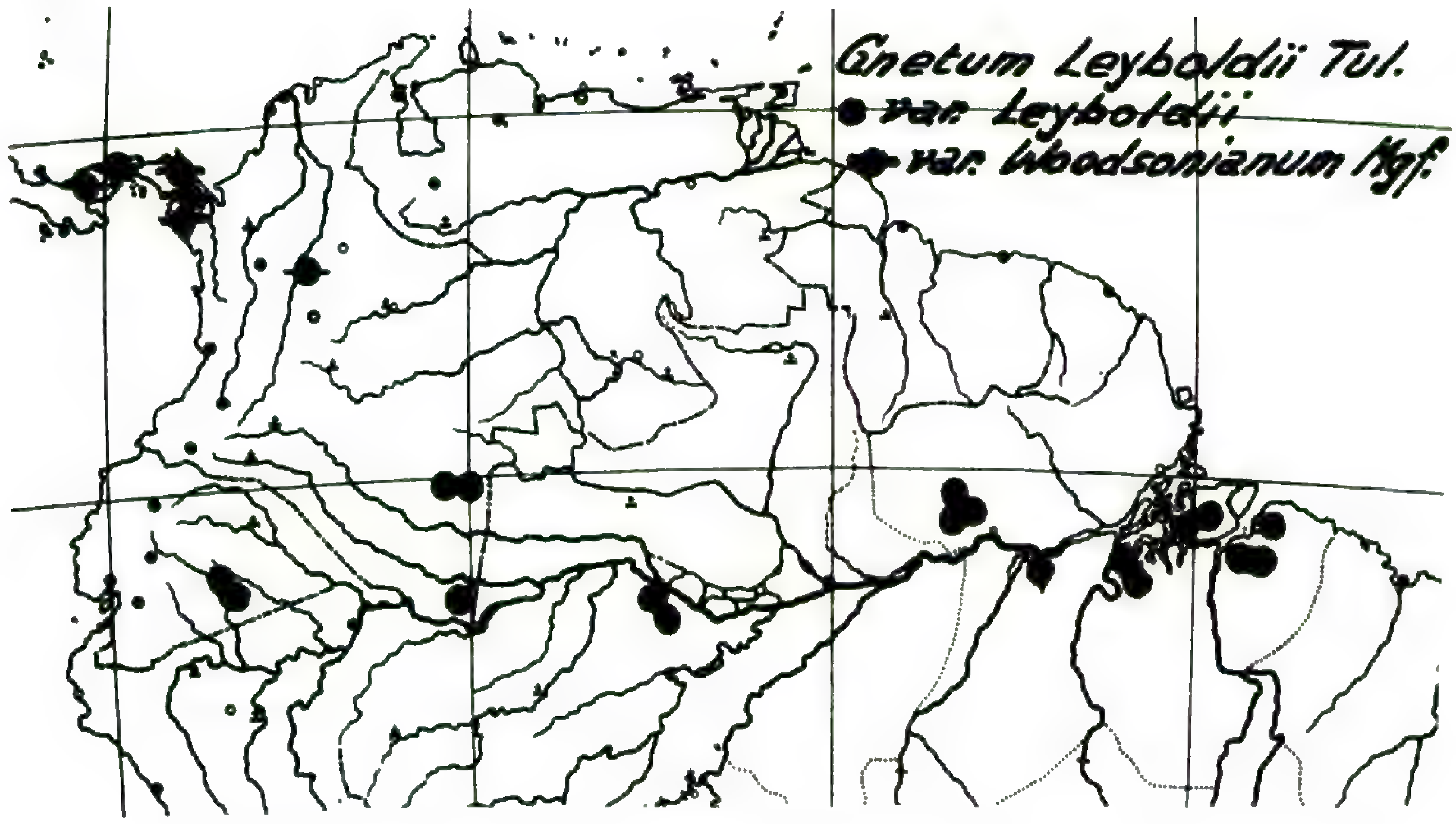
The respective areas of the species are documented by the following localities (see sketch maps).

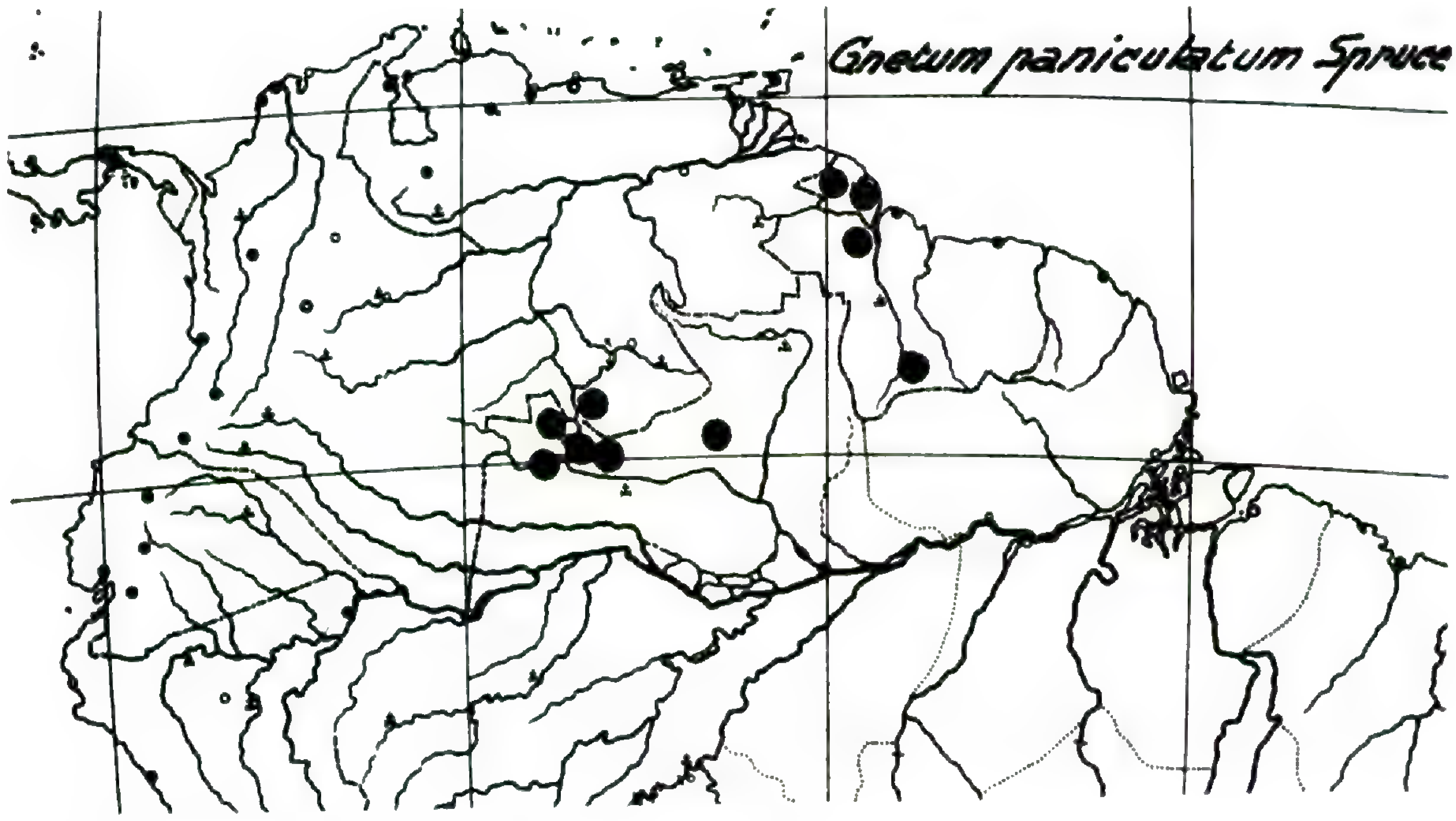
1. *Gnetum urens* (Aubl.) Bl., Tijdschr. Natuurl. Geschied. **1** (1834) 155. (*Thoa urens* Aubl., Pl. Guyane Franç. **2** (1775) 874; *Gnetum Thoa* R. Br. ex Brongn. in Duperrey, Voy. sur la Coquille (1829) 12; *G. Melinonii* Benoist, Bull. Mus. Hist. Nat. Paris 2 Sér. 17 (1945) 66).

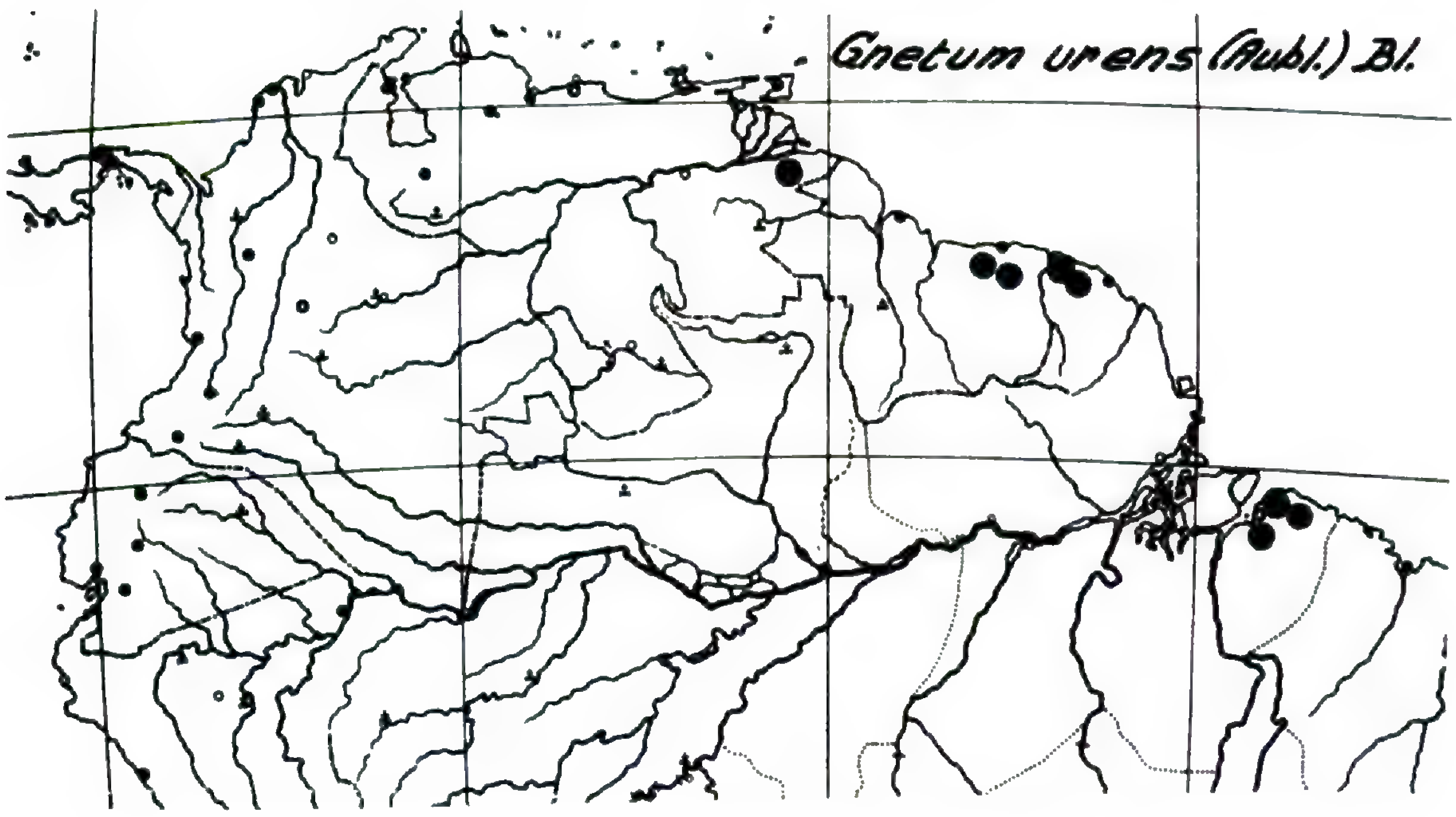
VENEZUELA: Catalina (lower Orinoco), ♂ fl, May 1896, *Rusby & Squires 424* (Z). SURINAME: Bergendal at the Suriname River, ♂ fl, *Focke 1314* (U); Saramacca River, ♂ fl, *Weigelt ?* (G). FRENCH GUIANA: Acarouany (NW), fr, 1855, *Mélinon* (G), *Sagot 493* (P); Maroni, *Mélinon* (P). NORTHERN BRAZIL: PARÀ: Bragança, Colonia Benjamin, in silva secundaria, fr, 17.11.1908, *Ducke 19410* (RB); Estrada de Tracuatena, capoeira, fr. 11.6.1952, *Fróes 28489* (IAN); Municipio de João Coelho, estrada de ferro de Bragança, capoeira, fr, 13.5.1956, *Ferreira* (IAN); Belém. mata do mocambo IAM, fr, Nov 1951, *Black 51-14108* (US).

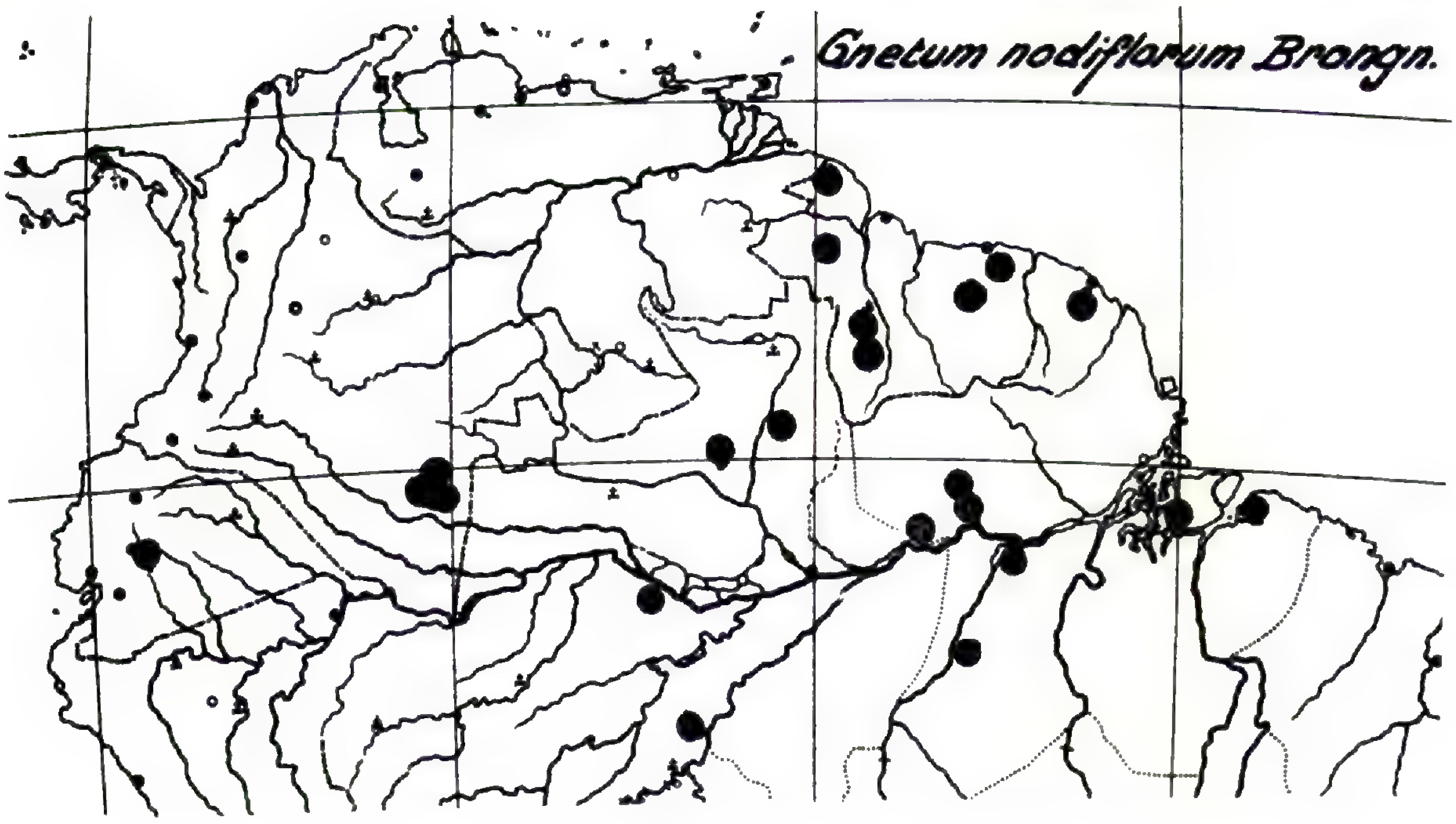
2. *Gnetum nodiflorum* Brongn. in Duperrey, Voy. sur la Coquille (1829) 12. (*G. amazonicum* Tul., Ann. Sc. Nat. 4 Sér. **10** (1858) 116; *G. Cruzianum* Gleas., Bull. Torrey Bot. Cl. **52** (1925) 196.)

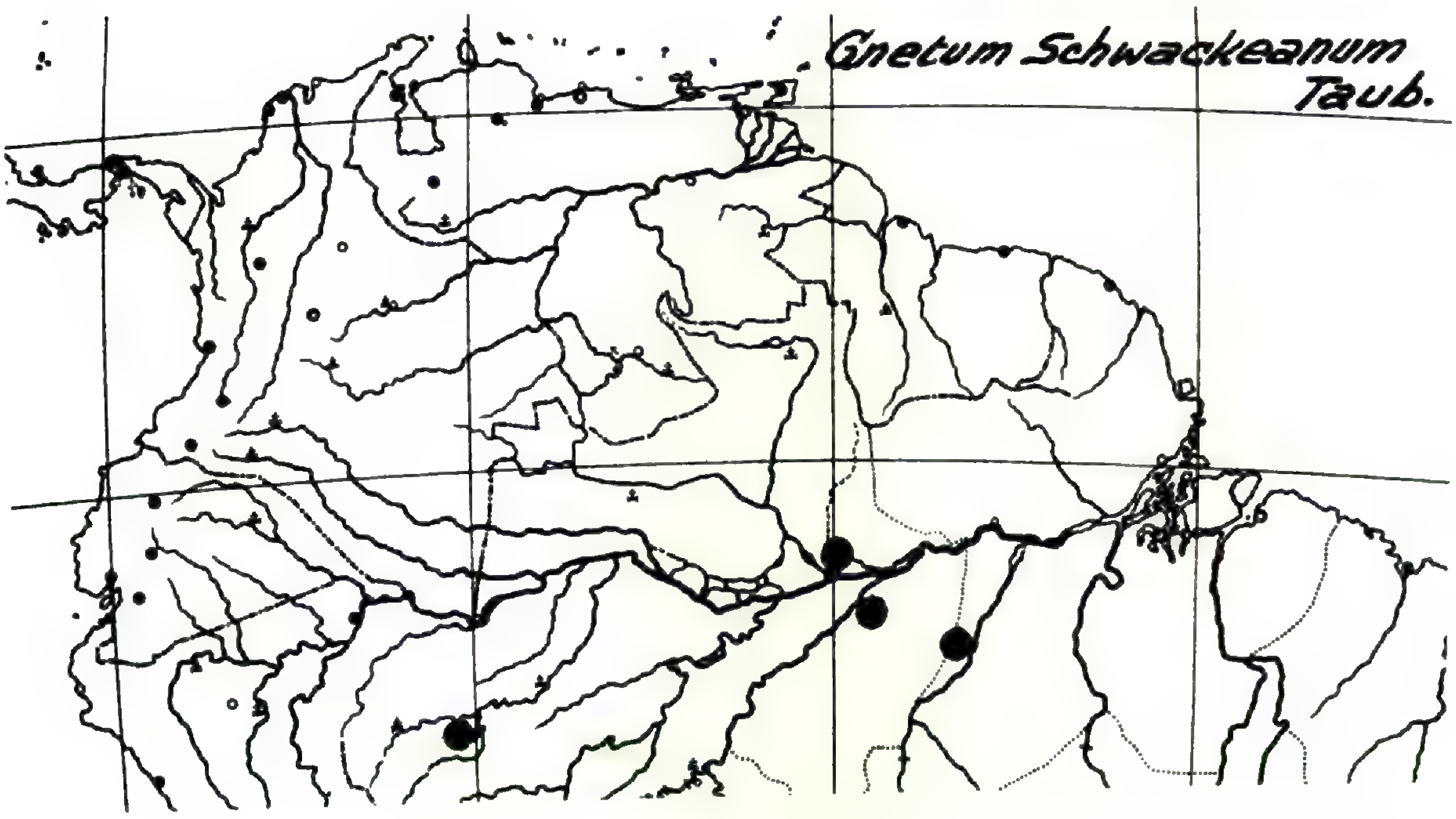
BRITISH GUIANA: Amakura River (NW), ♂ fl, *De La Cruz 3522* (NY); Kamakusa, Mazaruni River, 59°50′W, ♂ fl, July 1923, *De La Cruz 4222* (NY); Sandige Savanne am Demerara, ♂ fl & fr, Apr 1844, *Rich. Schomburgk 1013* (W); Rupunini River, Isherton, fr, 1937, *A. C. Smith 2420* (K); Moraballi Creek, fr, 1929, *Sandwith 531* (K); Kanuku Mts., Wabuwak, 600 m, ♀ fl & fr, Oct 1948, *Wilson Browne 5738* (K). FRENCH GUIANA: Cayenne, ♂ fl, 1819/21 *Poiteau* (G, Isotype); ♂ fl, 1821, *Perrottet 176* (G). NORTHERN BRAZIL: PARÀ: Região de Ariramba, Campo do Mutum, á beira do campo, ♂ fl, 28.5.1957, *Black, Egler, Cavalcante & Silva 57-19672* (IAN); Ilha de Colares, municipio de Vigia, Sítio Horizonte, fr, 29.9.1954, *Black 54-16935* (IAN); Municipio de Breves, perto do Igarapé Arapigó, fr. 5.11. 1958, *Guedes 661* (IAN); Bellavista, lower Tapajoz River, in campis arenosis apertis, Campina do Perdido, unterhalb der Cachoeira Maranhãozinho, fr, 12.9.1916, *Ducke 19406* (RB); Cunani, fr, 13.10.1895, *Huber 1031* (MG, G); Santarem Alto do Chão, silva non inundata, ♀ fl, 22.6.1910, *Ducke 10821* (MG); Obidos, ♀, Jan 1921, unknown collector (RB). AMAZONAS: ad ripam Lago Faro, ♀, 3.9.1907, *Ducke 8581* (MG); Vista Alegre, no meio Rio Branco, matas de Savanna, ♂ fl, March 1913, *Kuhlmann 2977* (RB); Cachoeira do Rio

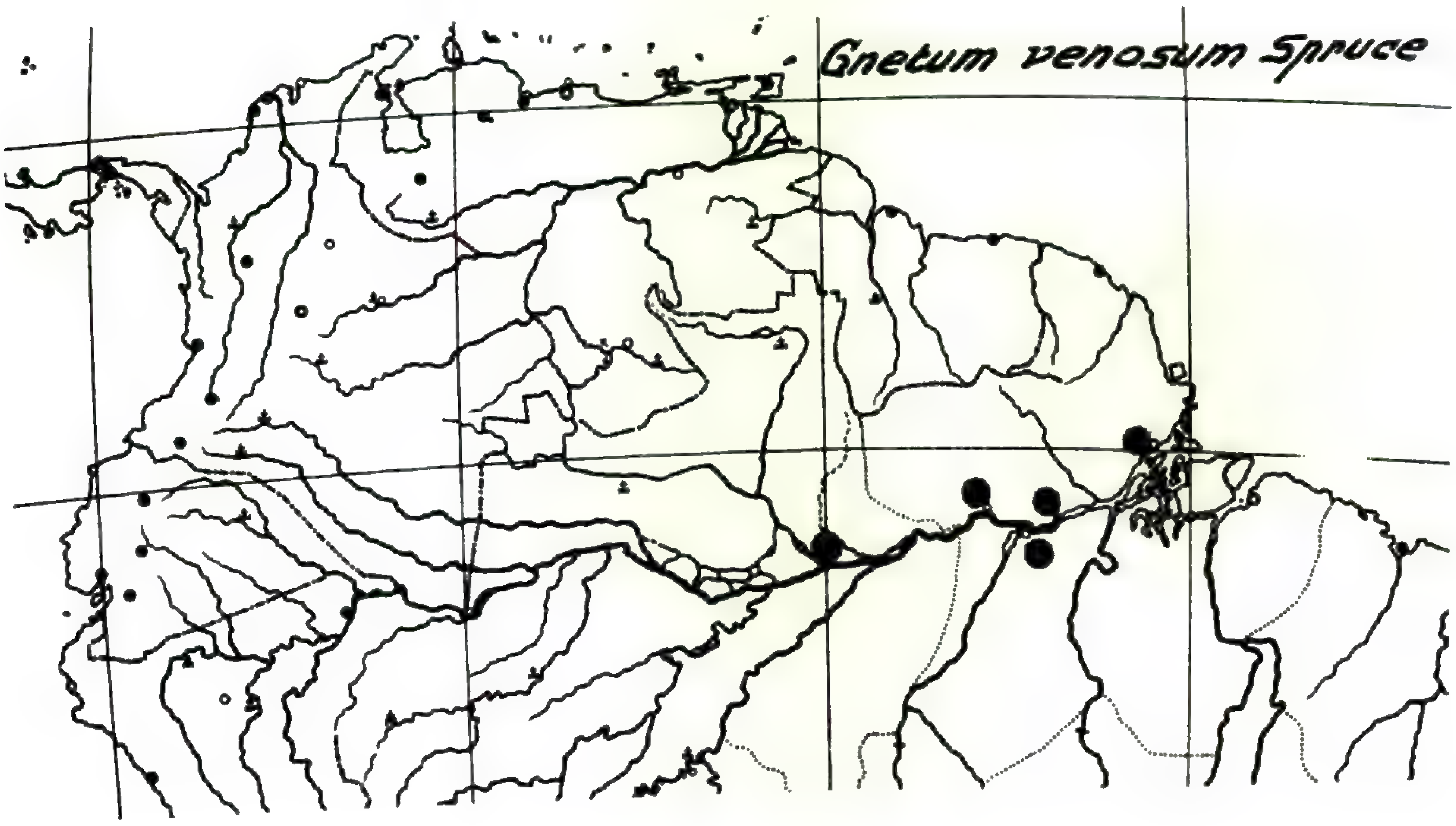

Gnetum Leyboldii Tul.
var. Leyboldii
var. Woodsonianum Mgf.


Gnetum paniculatum Spruce


Gnetum urens (Aubl.) Bl.


Gnetum nodiflorum Brongn.


Gnetum Schwackeanum Taub.


Gnetum venosum Spruce

Aracá, subafluente do Rio Negro, ♀ fl, 29.10.1952, *Froes & Addison 29179* (IAN); Ega (=Teffe), ♀, Sept 1831, *Poeppig 2601* (W.) Ecuador: Prov. Tungurahua, Rio Negro, fr, 9.11.1952, *Fagerlind & Wibom 1238* (LD). Colombia: Amazonas, Río Caquetá, La Pedrera, ♂ fl, July 1948, *Schultes & Lopez 10220A* (US); Amazonas-Vaupés, Rio Apaporis, Raudal Yayacopi (La Playa), 250 m, 0°5′S, 70°30′W, fr, 18.8.1952, *Schultes & Cabrera 16909* (US); Río Apaporis, Jinogojé (at mouth of Río Piraparaná) & vicinity, alt about 700 ft, 0°15′S, 70°30′W, fr, 27.2.1952, *Schultes & Cabrera 15667, 16656* (US); Rio Apaporis, entre el rio Pacoa y el rio Takunema, Cerro de la Hoz, alt ca 250 m, fr, 21.9.1951, *Schultes & Cabrera 14119* (US); Rio Apaporis Raudal de Jirijirimo (below mouth of Rio Kananarí), Quarzite base, 900 ft, 0°5′N, 70°40′W, fr, 15.3.1952, *Schultes & Cabrera 15932* (US); Rio Piraparaná (tributary of Rio Apaporis, lower course), between 0°15′S, 70°30′W and 0°25′N, 70°30′W, fr, 9.3.52, *Schultes & Cabrera 15921* (US).

3. *Gnetum paniculatum* Spruce ex Bentham in Hook., J. Bot. and Kew Gard. Misc. **8** (1856) 357. (*G. microstachyum* Spruce, loc. cit.)

British Guiana: Assakatta (NW), fr, *De La Cruz* (NY); Essequibo, ♂ fl, 1928, *Sandwith* (K); Moraballi Creek, *Sandwith 36, 376, 420, 527* (K); Barabara Creek, ♂ fl, For. Dept 3559 (K); Black Creek, ♂ fl, For. Dept 4525 (K); Demerara River, ♂ fl, *Jenman 6880* (K). French Guiana: Le Monnier (G.) Venezuela: Rio Guainia (upper Rio Negro) San Carlos, ♂ fl, 1853/4 *Spruce 1923* (K, holotype). Northern Brazil: upper Rio Negro São Gabriel, capoeiras, ♀, May 1852, *Spruce 2314* (K); *Panuré* (=Ipanoré), Rio Uaupès ♂ fl, 1852/3, *Spruce 2554* (K); Camatina, terra firme, 250 m, ♀ fl, 25.1.1949, *Fróes 24004* (K); Rio Içana, Estirao Santa Ana, fr, *Fróes 27982* (IAN); São Felipe, Rio Negro, Igarapé Tourí, igapó, ♂ fl, 27.9.1952, *Fróes 28780* (IAN); Cachoeira do Rio Acará, subafluente do Río Negro, á margem do rio, ♂ fl, 29.10.1952, *Fróes & Addison 29150* (IAN).

4. *Gnetum venosum* Spruce ex Bentham in Hook., J. Bot. and Kew Gard. Misc. **8** (1856) 358.

Northern Brasil: Parà: Rio Maicurú, municipio de Monte Alegre, terreno baixo, á beira do rio, fr, 15.9.1953, *Fróes 30236* (IAN); Macapá, silva riparia ad flumen Matopy, fr, 30.4.1926, *Ducke 19414* (RB); Santarem, Varzea forest nr Tapeirinha, fr, Dec 1938, *Markgraf 3898;* Lago Salgado, Rio das Trombetas, margem da mata, fr, 20.3.1924, *Kuhlmann 19044* (RB). Amazonas: Manáos, on river Solimões, ♂ & ♀ fl, 12.7.1882, *Schwacke III 567* (=*Glaziou 14284!*); Manáos, S bank of Rio Negro, ♂ fl, May 1851, *Spruce 1579* (K, holotype).

5. *Gnetum Schwackeanum* Taubert ex Markgraf, Bull. Jard. Bot. Buitenzorg 3 Ser. **10** (1930) 450.

Northern Brazil: Parà: Furnas (middle Tapajoz River), silva non inundata, fr, 11.9.1916, *Ducke 16474* (MG). amazonas: Manáos, forest Cua reté, ♂ fl, 15.7.1882, *Schwacke III 788* (=*Glaziou 14285*, type); Manáos, capoeira Cachoeirinha, ♀ fl, 3.8.1900, *Ule 5310*; Manáus, mata da terra firme em direção ao Rio Tarumá, fr, 8.3.1946, *Ducke 1927* (K); Rio Madeira, Rio Canumã, cipó sôbre árvores isoladas na campina-rana, fr, 5.11.1957, *Fróes 33762* (IAN). acre: mouth of Rio Embira, fr, 1933, *Krukoff 5065* (K).

6. *Gnetum Leyboldii* Tul., Ann. Sc. Nat. 4 Ser. **10** (1858) 115. (*G. paraense* Hub., Bot. Museu Paraense **3** (1902) 403.)

a) var. *Leyboldii.*

Northern Brazil: Parà: Collares, silva riparia ad flumen Parà, ♂ fl, 19.8.1913, *Ducke 19409* (RB). Marajó: in silva igapó ad flumen Anajaz, ♀ fl, 21.8.1926, *Ducke 19407* (RB); Breves, Furo Macuyubim, ♂ fl, 30.8.1901, *Guedes 2214* (MG); Rio Acarà, Thomé assú, 45 m, fr, 27.7.1931, *Mexia 6000* (Z); Rio Jaraucu (Xingú), Porto de Móz, á beira do rio, fr, 11.10.1955, *Fróes 32191* (IAN); Beira do Rio Curuaúna, várzea, região do planalto de Santarém, ♀ fl, Oct 1954, *Fróes 31343* (IAN); Região de Anapú, Rio Maparauá, Portel, à beira do rio, ♀ fl, 5.8.1956, *Fróes 32935* (IAN); Região de Anapú, Rio Flexal, Portel, á beira do

rio, young fr, 30.9.1956, *Fróes 32758* (IAN) Região de Anapú, Rio Pracajaí, Portel, á beira do rio, young fr, 14.9.1956, *Fróes 32746* (IAN); Beira do Rio Mapuá, várzea, entre Vila Emilia e Bôca do Mapuá, ♂ fl, 18.7.1950, *Black, Fróes & Ledoux 50-9801* (IAN); Antonio Lemos, várzea, Igarapé Pixuna, muito comun, ♂ fl, 18.7.1948, *Black 48-2967* (IAN); Rio das trombetas, Mittellauf, am Ufer der Stromschnellen des Flusses Jaramacarú, ♀ fl, 11. 10.1913, *Ducke 19408* (RB); Rio das Trombetas, Unterlauf, am Ufer der Stromschnellen des Flusses Mapuera, fr, 5.12.1907, *Ducke 9044* (MG). AMAZONAS: Humaytà, border of Rio Ipixuna between Monte Christo and Santa Victoria, fr, *Krukoff 7264* (K); Ega (=Teffe), im feuchten Urwald, ♂ fl, Nov 1819, *Martius* (M, type); In Wäldern bei Nogueira (westl. Ega) fr, Dec 1819, *Martius* (M); In den Wäldern am Fluss Yapurá (bei Ega) fr, Jan 1820, *Martius* (M); Rio Caipurù, *fr. Spruce* (K). ECUADOR: Prov Tungurahua, Rio Negro, forest on shore of Rio Pastaza, 1200 m, ♂ fl, 25.8.1939, *Asplund 8558* (S); Prov Tungurahua, Rio Negro, Uferwald am Rio Pastaza, 1200 m, ♂ fl, 26.9.1955, *Asplund 18638* (S); Prov Tungurahua, Rio Negro, ♂ fl, 9.11.1952, *Fagerlind & Wibom 1236a & b* (LD). COLOMBIA: Amazonas, Rio Mirití-Paraná, 0°30′S, 70°40′W, 200 m, fr, 8.5.1952, *Schultes & Cabrera 16412* (US); Amazonas-Vaupés, Rio Apaporis, Cachivera de Jirijirimo, 250 m, fr, 7.7.1951, *Schultes & Cabrera 12973* (US); Amazonia, Ufer des Rio Loreto-Yaco, Várzea-Wald, fr, 1.11.1946, *Schultes & Black 46-268* (US); Vaupés, Lobo Igarapé, Oberlauf des Caño Teemeeña (Rio Pira-paraná, Nebenfluss des Rio Apaporis), zwischen 0°15′S, 70°30′W & 0°25′N, 70°30′W) fr, 10.9.1952, *Schultes & Cabrera 17339* (US).

b) var. **Woodsonianum** Mgf., var. nov.

COLOMBIA: Dept Santander, vic of Porto Berrio, Carare valley, 100-700 m, ♂ fl, 22.4.-1935, *Haught 1662* (US). PANAMA: High hills back of Puerto Obaldéa, San Blas coast, 50-200 m, fr, Aug 1911, *Pittier 4317* (US); Bismarck, above Penonome, fr, 18.3.1908, *Williams 608* (US), vic of La Palma, southern Darien, 0-50 m, fr, Jan/Febr 1912, *Pittier 5488* (US); Boco de Panarandó, on Sambú River, southern Darien, alt 20 m, fr, Febr 1912, *Pittier 5685* (US); NW Canal Zone, W of Limon Bay, Gatun Locks & Lake, IWTC headquarters, ♂ & ♀ fl, fr. 5.4.1956, *Johnson 1786* (MO).

Frutex alte scandens dioicus. Truncus lignosus, ad 10 cm crassus, ligno ex anulis annorum 5 mm latis latiporis constructo, cortice griseo, aspero, lenticellis magnis percusso obtectus. Ramuli teretes, graciles, laeves. Folia opposita, petiolus 1 cm longus, lamina late ovata, acuta vel breviter acuminata, 9-15 cm longa, 5-10 cm lata, plerumque 10 cm longa, 6 cm lata, laete viridis, fibris crebris oblique parallelis, supra conspicuis sericeo-nitens, nervi laterales 1 cm inter se remoti, arcuati, 5-7 in utroque latere, 6-8 mm ante marginem coniuncti, subtus prominuli. Inflorescentiae ♂ axillares, semel vel bis ramificatae, uni- vel binodae internodiis gracilibus, primi ordinis ad 4 cm longis, e bracteis nodalibus 2 oppositis ovato-acuminatis, 3-5 mm longis spicas 2-4(-5) emittentes, spica una apicali terminatae. Spicae adultae 2 cm longae, 6-7 collibus cyathiformibus, basin versus angustatis, 3 mm altis et 2 mm latis, 2 mm inter se distantibus ornatae. In quoque collo multi flores lutei masculini et nonnulli feminini steriles pilis immersi. Perianthium masculinum obconicum, angulatum, 0.7 mm longum, 0.3 mm latum; stamen unicum 1 mm longum, exsertum, filamentum a dorso compressum, antherae 2 apicales, oblongae, rima brevi apicali apertae. Florum femineorum sterilium involucrum externum clavatum 0.7 mm longum 0.3 mm latum, involucrum internum brevius, tenerum, supra medium latissimum. Inflorescentiae ♀ graciles, semel ramificatae, internodiis apicem versus cito brevioribus (ab 1 cm ad 2 mm) collibus 3-5, iuvenilibus cyathiformibus, adultis dilatatis et tum vix 1 mm altis, 2 mm latis ornatae. Flores feminei fusco-lutei, subglobosi, perianthium ½ mm altum et latum, involucrum medium crassiusculum, intimum globosum, minus (tantum mediam altitudinem involucri medii attingens), in tubulum apicalem brevem, vix exsertum

angustatum. Fructescentiarum internodia ad 1½ cm elongata, 2 mm crassa. Semina matura oblonga, marginibus parallelis, utrimque rotundata, apice minute apiculata, 4.5-5 cm longa, 2 cm lata. Involucrum externum rubrum, satis carnosum, 1 mm crassum, medium laeve, chartaceum, fasciculis fibrorum remotiusculis longitudinaliter signatum, intimum tenue, nucellus 3 cm longus, 13 mm latus.

Distribution: Panama to SW Colombia. Localities see above. Type specimen: *Ivan M. Johnston 1786* (MO); composite specimen, consisting of twigs with young ♂ flowers, twigs with ♀ flowers & twigs with fruits. For well developed ♂ flowers, see *Oscar Haught 1662* (US).

DISTRIBUTION PATTERNS OF CERTAIN UMBELLIFERAE[1]

BY MILDRED E. MATHIAS

Department of Botany, University of California, Los Angeles

In a Miscellany in Honor of Merrit Lyndon Fernald, Woodson (1947) discussed the "Historical Factor" in plant geography. Now almost twenty years later it seems appropriate to continue the discussion in a miscellany in honor of Robert Everard Woodson. For years Woodson was intrigued by the relations of paleography to present patterns of distribution and variation, particularly of *Apocynaceae* and *Asclepiadaceae*, and we engaged in many discussions on possible interpretations of Angiosperm distributions.

The Angiosperm family *Umbelliferae* is cosmopolitan primarily in temperate areas where it exhibits many interesting patterns of distribution and variation (Fig. 1, 2, 3, 4). Even though the fossil record for the family is inadequate it may be informative to generalize and speculate on the evolution of some of the present distributional patterns.

The two families *Araliaceae* and *Umbelliferae* are a closely related and natural group probably derived from a pro-araliaceous stock. Baumann's (1946) comparative study of the fruit of the New Caledonia genus *Myodocarpus* (*Araliaceae*) and of the *Umbelliferae* supports this view and indicates that the *Umbelli-*

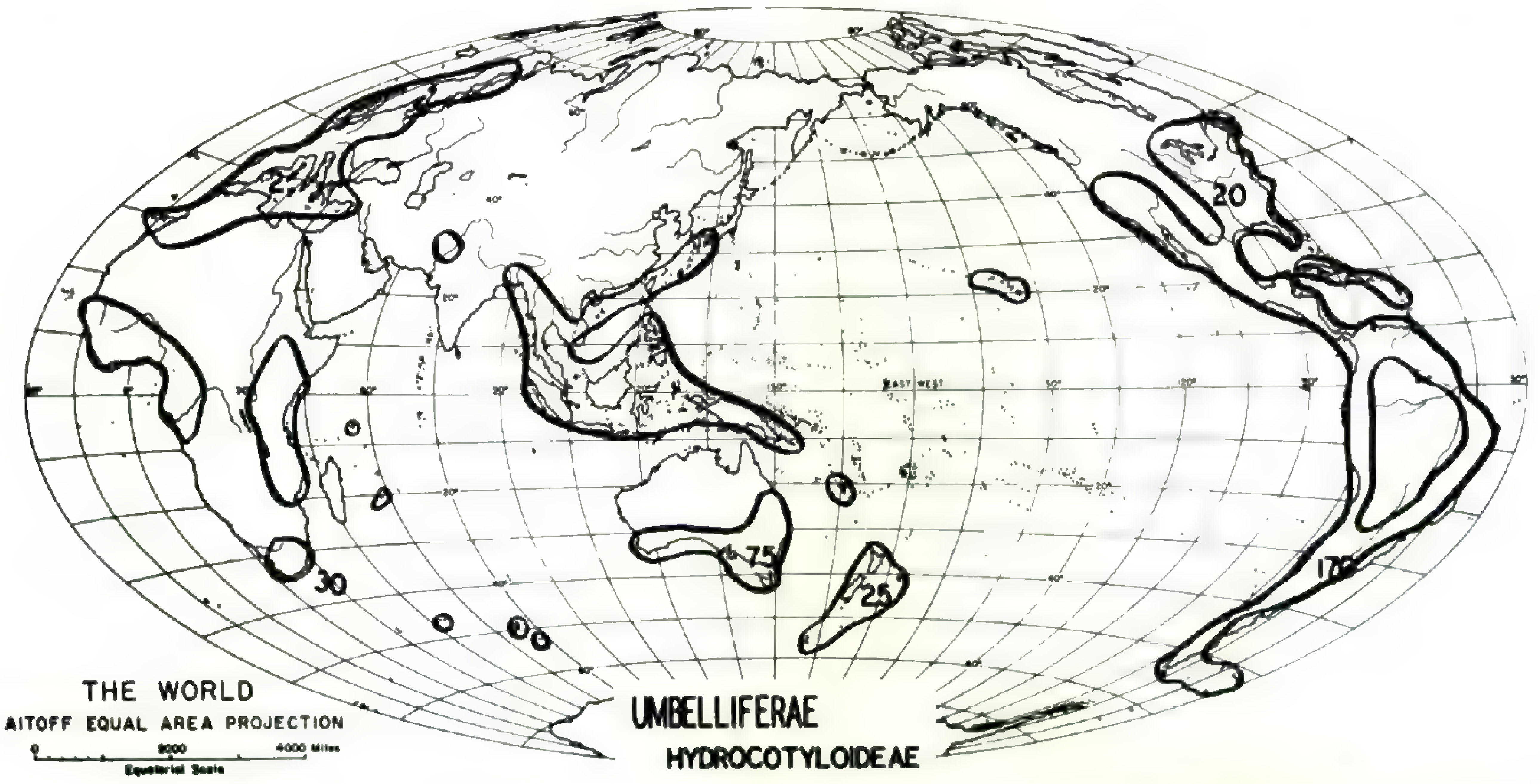


Fig. 1. Distribution of the subfamily *Hydrocotyloideae, Umbelliferae* (320 species). Numbers indicate the approximate number of species for each area.

[1] This brief review is a summary of ideas developed over a period of years while conducting taxonomic studies on the American *Umbelliferae* supported by the New York Botanical Garden, the Committee on Research, University of California, Los Angeles, and the National Science Foundation (G-13393 and GB-1293). Many individuals have assisted in the collection of data, preparation of maps, etc. Among them I wish to thank especially Miss Jane Turner, Mr. Allan Andrews, and Mrs. Mimi Lonski, all of the University of California, Los Angeles.

ANN. MISSOURI BOT. GARD. **52**(3): 387-398. 1965.

ferae is the more advanced of the two families. The anatomical study of Rodriguez (1957) sustains the thesis that the two families have diverged from a single ancestral source and indicates that, of the tribes of the *Araliaceae*, the *Mackinlayeae* appear to be closest to the *Umbelliferae*. Recent studies by Tseng (1965) on fruit anatomy and pollen morphology present further data to show the probable derivation of the *Araliaceae* and *Umbelliferae* from a common stock.

The modern *Araliaceae* have a wide distribution with a concentration of species in the tropics (Fig. 5). While no taxonomic summaries of the entire family have appeared in recent years those of Harms (1898) and Viguier (1906) give us a general idea of the areas of differentiation and general distribution. Of the some 600 species about 400 occur in tropical areas and only 200 in temperate regions, approximately equally distributed in the northern and southern hemispheres. Harms described three tribes—the *Scheffiereae*, in the tropics of all hemispheres with some species extending into temperate regions, one (*Oplopanax horridum*) into western North America; the *Aralieae*, occurring equally in tropical and temperate areas but unknown from Europe and Africa; and the *Mackinlayeae*, all tropical or subtropical in Queensland and New Caledonia. Viguier (1906) recognized ten tribes, all but one of which is represented in the tropics and subtropics of New Guinea, New Caledonia, and eastern Australia.

The *Araliaceae* has long been recognized as an ancient Angiosperm family, and it is well known in the fossil record of the Cretaceous (Axelrod, 1952). About 60 taxa in eight genera have been described from the Cretaceous of North America, some 40 of which have been assigned to the modern genera *Aralia*, *Hedera*, and *Panax*. The tribe *Scheffiereae* is represented in the Tertiary floras of North America with 13 taxa in three genera and the *Aralieae* with 38 taxa in three genera (Table 1). The fossil record indicates that the *Araliaceae* were a component of the tropical Tertiary geofloras (Axelrod, 1952). From the present distributions we may infer a probable origin for the family in the paleotropics where some 200 species now occur in Indo-Malaysia, northeastern Australia, and New Caledonia. It is here that we find *Myodocarpus* and taxa assigned to the *Mackinlayeae*, those which show the closest affinity in fruit and wood anatomy to the *Umbelliferae* and which are probably most closely related to the pro-araliaceous stock. The modern temperate elements of the family represent survivors of subtropical taxa which extended father north in the Tertiary (Chaney, 1947).

The generalized distribution pattern for the *Umbelliferae* shows a clear relationship to that of the *Araliaceae* but reflects the more temperate requirements of the family. Where species occur in tropical latitudes they are, except for a few weedy representatives, confined to high montane temperate or even subalpine habitate. Three subfamilies have been distinguished by students of the family. The *Hydrocotyloideae* (considered a family by Hylander, 1945) consists of some 320[2]

[2] Approximate numbers of species in each subfamily and for areas of the world outside the western hemisphere have been based on compilations largely from Drude (1898) and Willis (1951). It is impossible with the present information on the family to arrive at more than approximations. However it is believed that relative proportions of taxa will not be changed significantly as investigations proceed.

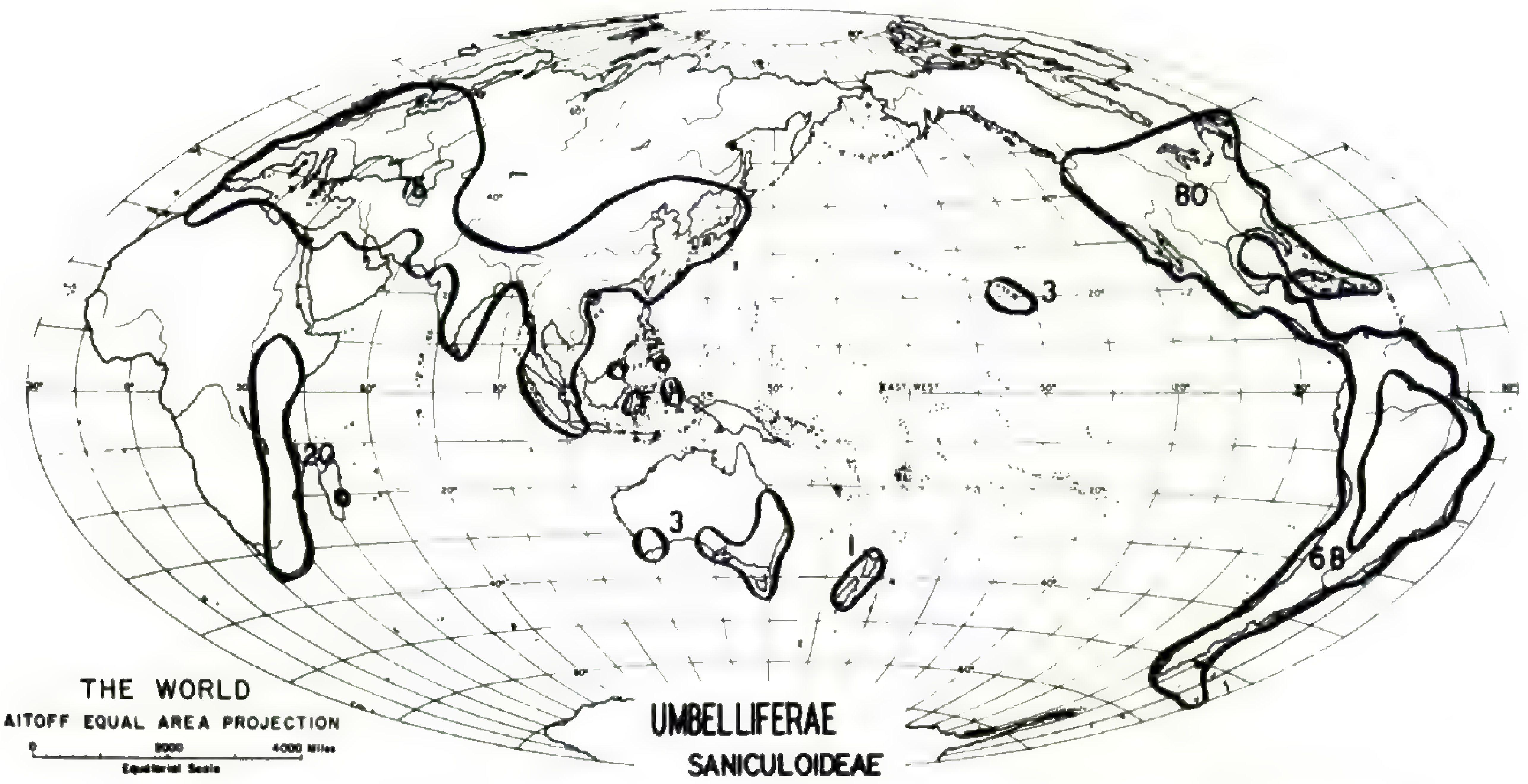


Fig. 2. Distribution of the subfamily *Saniculoideae, Umbelliferae* (250 species). Numbers indicate the approximate number of species for each area.

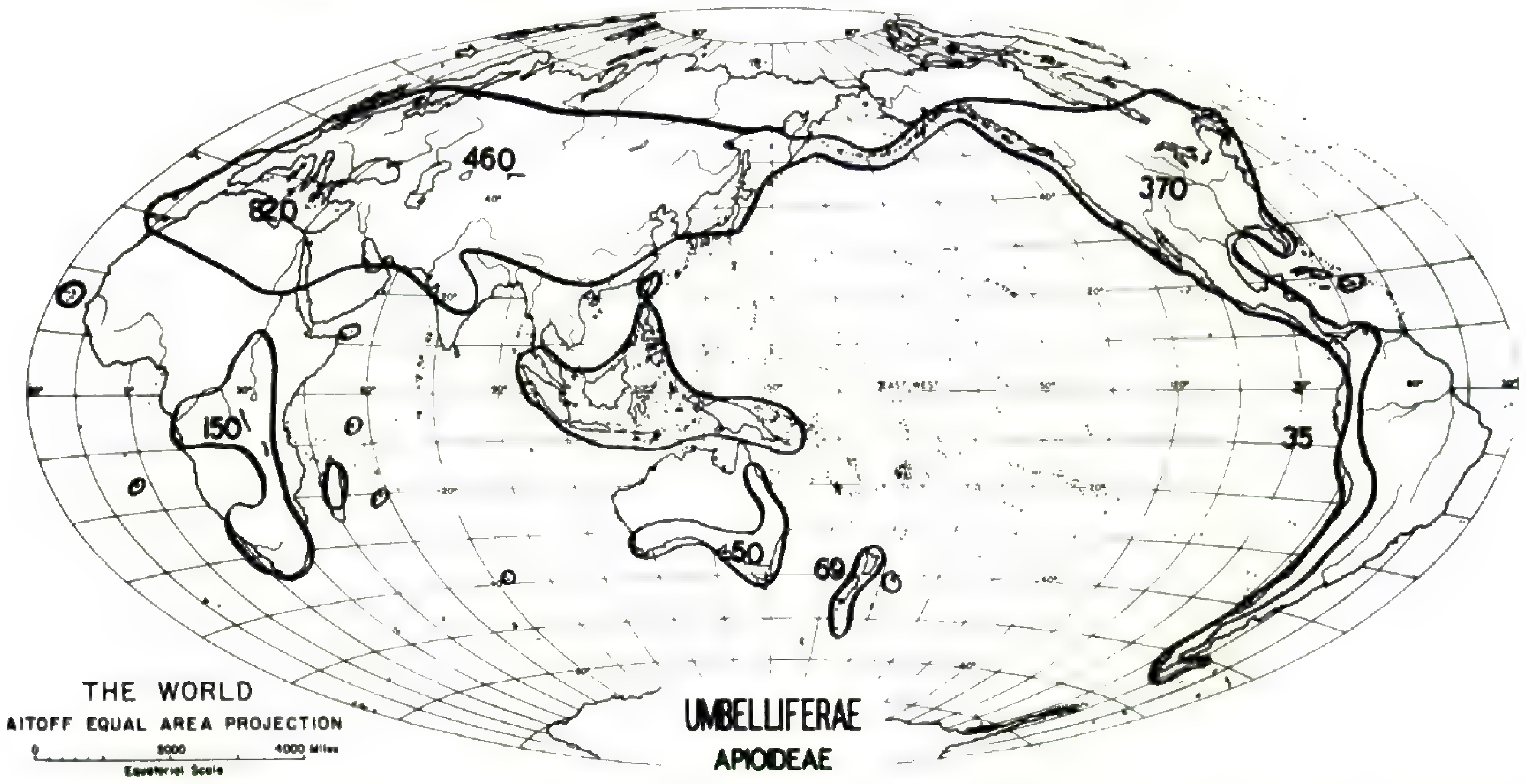


Fig. 3. Distribution of the subfamily *Apioideae, Umbelliferae* (1950 species). Numbers indicate the approximate number of species for each area.

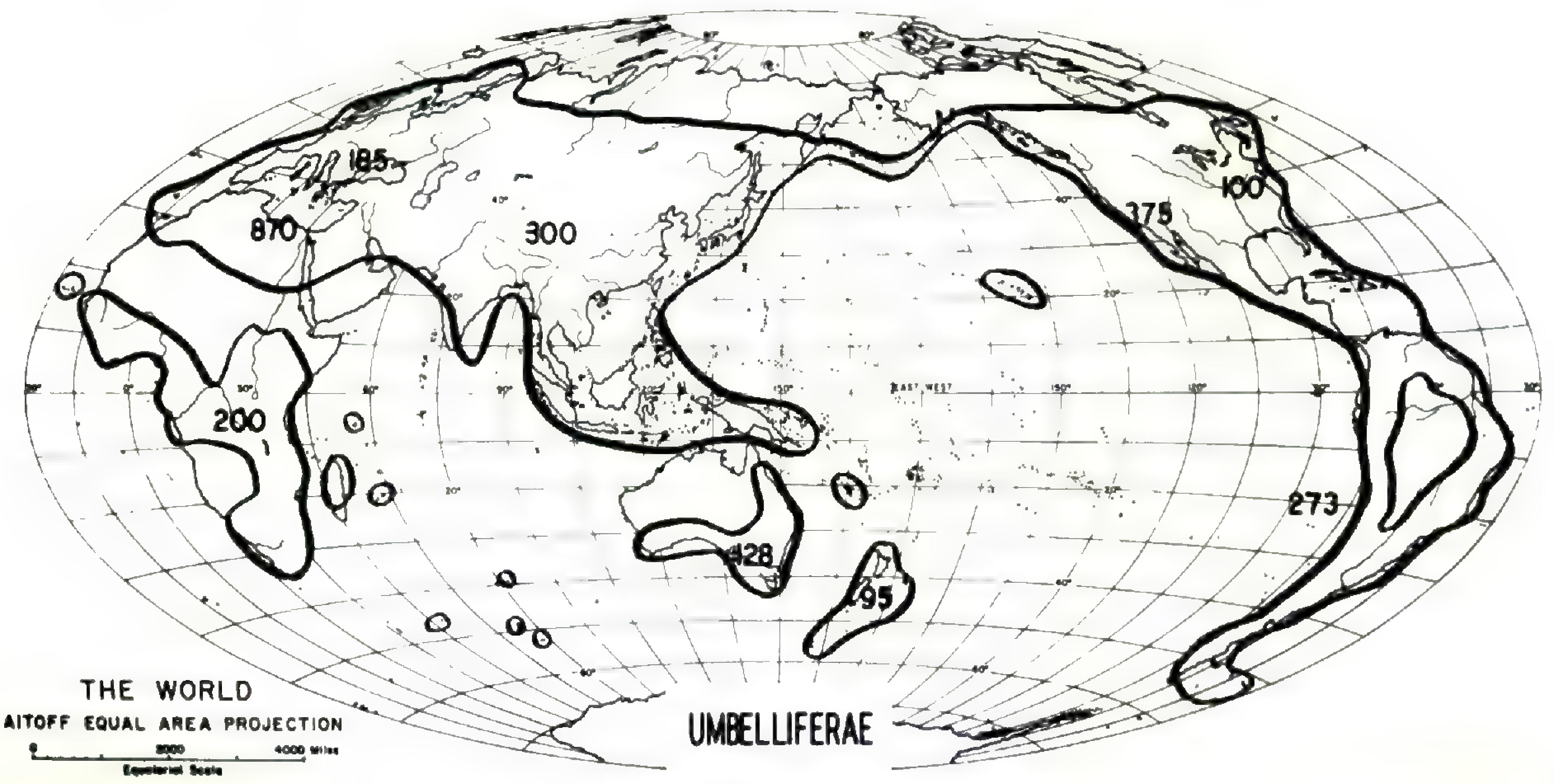
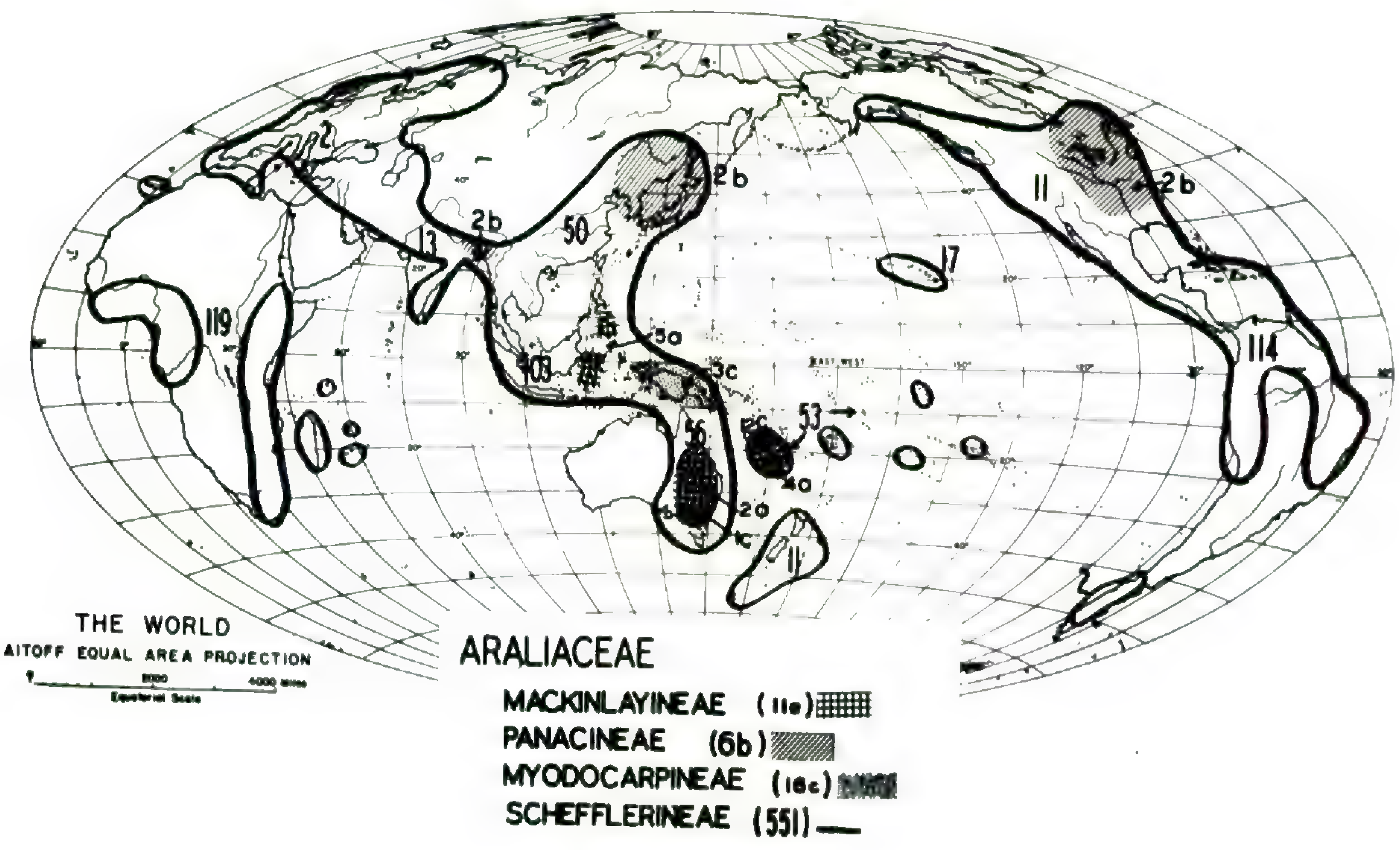


Fig. 4. Areas of differentiation for the *Umbelliferae*. Numbers indicate the approximate number of species for each area.



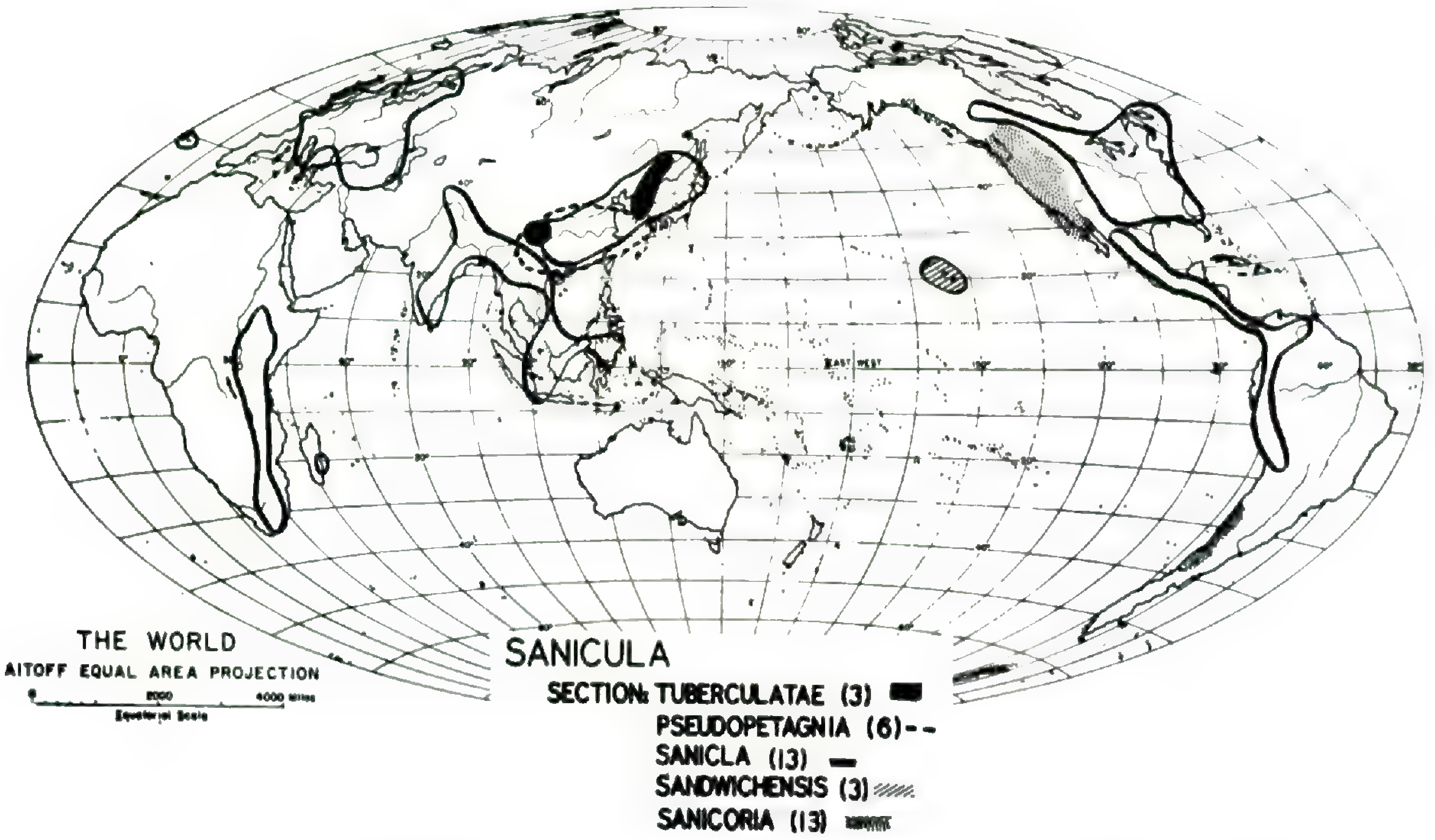


Fig. 5 (top). Distribution of the *Araliaceae* (600 species). Numbers indicate the approximate number of species for each area and have been derived from Harms (1898), Viguier (1960), and Willis (1951). Fig. 6 (bottom). Distribution of the sections of the genus *Sanicula* (38 species).

species and reaches its maximum differentiation and distribution in the southern hemisphere (Fig. 1). Of the some 30 genera only five have species which range into the northern hemisphere and these are all weedy or aquatic, possibly representing geologically recent invasions. The other two subfamilies, *Saniculoideae* (250 species) and *Apioideae* (1950 species) are bipolar in distribution but reach their maximum development in the northern hemisphere (Fig. 2 & 3). Figure 4 shows two modern centers of differentiation for the family, one in the Mediterranean area

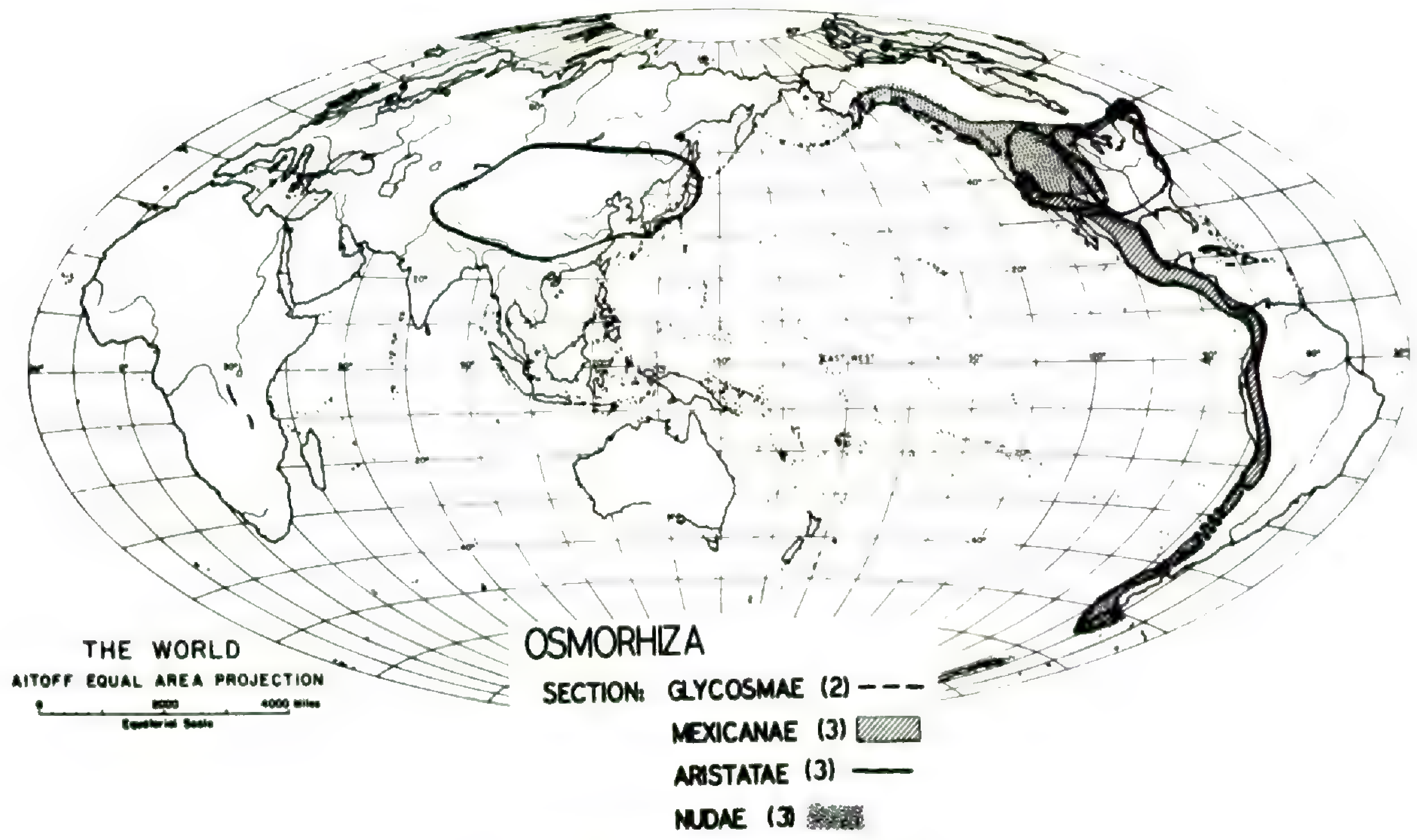
where some 900 species have been recognized and the other in the western United States and Mexico with 375 species. Since the taxonomy of the western North American genera has been under intensive study for several decades this paper will emphasize distribution patterns displayed in this second area of differentiation.

The subfamily *Hydrocotyloideae* is represented in western North America by a limited number of species, most or all of which show southern hemisphere affinities. As indicated above these may represent geologically recent incursions into the flora and consequently have been omitted from this discussion. Continued taxonomic study of the entire subfamily is in progress to clarify both morphological relationships and distributional patterns.

The subfamily *Saniculoideae* is represented in western North America by two genera, *Sanicula* (Fig. 6) and *Eryngium*. The 14 species of *Sanicula* occurring in the Pacific Coast states and Baja California belong to the section *Sanicoria*. Shan & Constance (1951) have described their present distribution and their possible evolution in response to changing climatic conditions since the Tertiary. Raven & Mathias (1960) further discussed the possible evolution of the section *Sanicoria* and concluded that this section apparently stemmed from ancestors adapted to relatively mesic sites within the area of the Arcto-Tertiary Geoflora but occupied successively drier and drier habitats offered by the expansion and differentiation of the Madro-Tertiary Geoflora. Constance (1963) has subsequently commented on the disjunct distribution of two species, *S. crassicaulis* and *S. graveolens*, between Pacific North America and Chile. Only one other species, *S. liberta* of the section *Sanicla*, occurs in western North America, extending from Chihuahua, Mexico to the Andes of Peru and Bolivia. Shan & Constance (1951) believe this species to be a southerly migrant from a widely ranging northern stock.

The genus *Eryngium* presents a much more complex pattern and one for which additional taxonomic and distributional data are needed. The relationship of the taxa of the New and Old World has not been satisfactorily investigated and it is only in recent years that sufficient material has been secured to begin a taxonomic study of the New World taxa. A number of polyploid species are known and Bell (1959) has suggested a correlation between the occurrence of polyploidy and certain distribution patterns. The species which occur in the Pacific Coast states occupy specialized habitats in salt water marshes or pools, freshwater marshes, vernal pools, or seasonally wet meadows.

The largest number of taxa of *Umbelliferae* in western North America belong to the subfamily *Apioideae*. The present distribution of many genera is holarctic and suggestive of a former close affinity with the Arcto-Tertiary Geoflora. This group may be exemplified by the genera *Osmorhiza, Sium, Ligusticum, Heracleum, Angelica,* and *Conioselinum,* all of which have representatives in the California flora. Constance & Shan (1948) in their revision of the genus *Osmorhiza* (Fig. 7) called attention to the occurrence of species of the section *Aristatae* in eastern North America and in eastern Asia, a familiar and well-documented pattern indicative of Arcto-Tertiary relationships. Constance (1963) has further commented on the disjunct distributions between Pacific North America and South America for



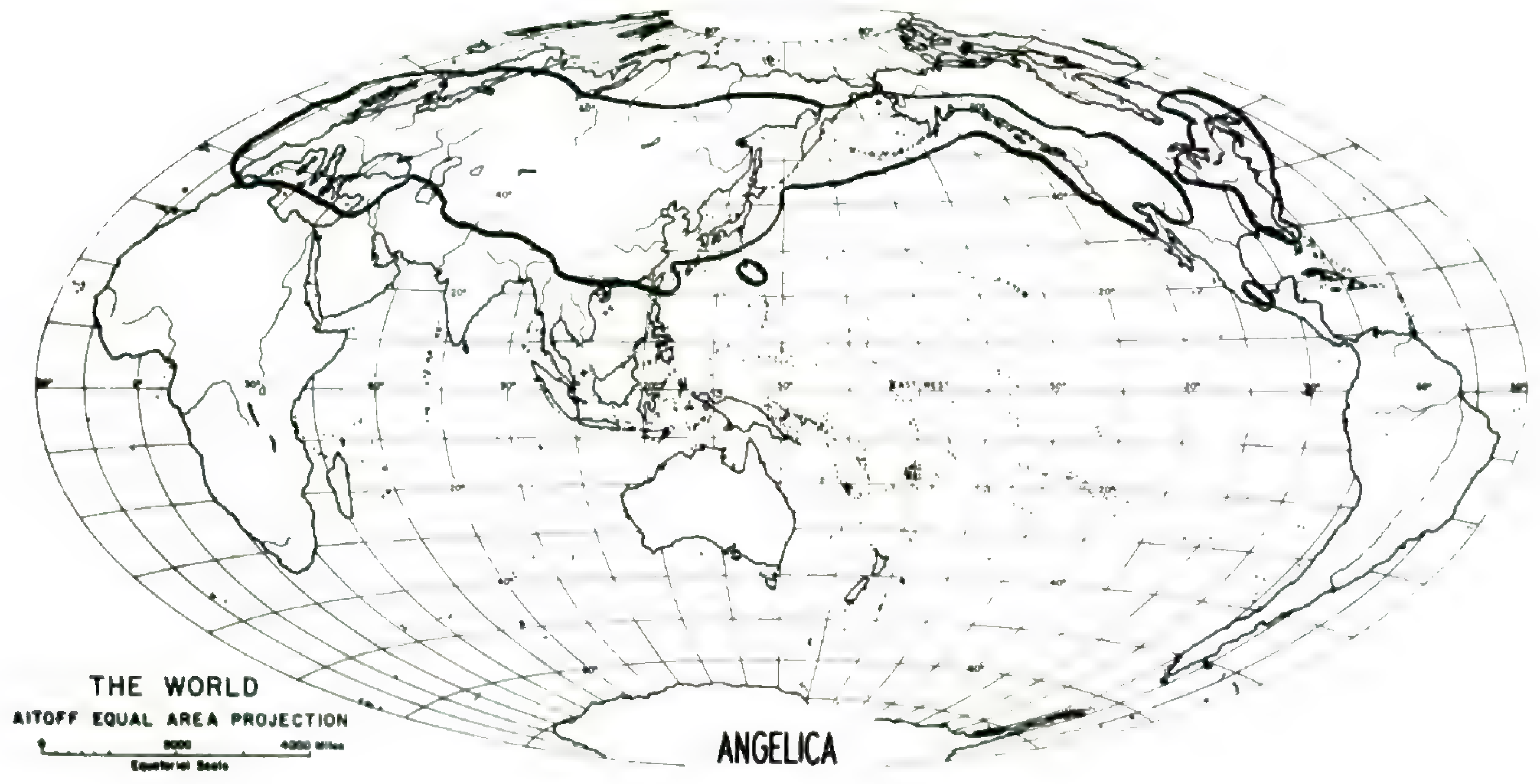


Fig. 7 (top). Distribution of the sections of the genus *Osmorhiza* (11 species). Fig. 8 (bottom). Distribution of the genus *Angelica* (50 species). The five species for New Zealand in H. H. Allan, Flora of New Zealand, 1961, have not been included. It is believed that they constitute a distinct genus *Gingidium* (Dawson, John W., A revision of the genus *Anisotome*. Univ. Calif. Publ. Bot. **33:** 6. 1961).

three species, distributions reminiscent of those occurring in *Sanicula*. The genus *Angelica* may be considered typical of the remaining genera listed above. Figure 8 shows its holarctic distribution, the species generally occupying mesic sites often along the margins of forests.

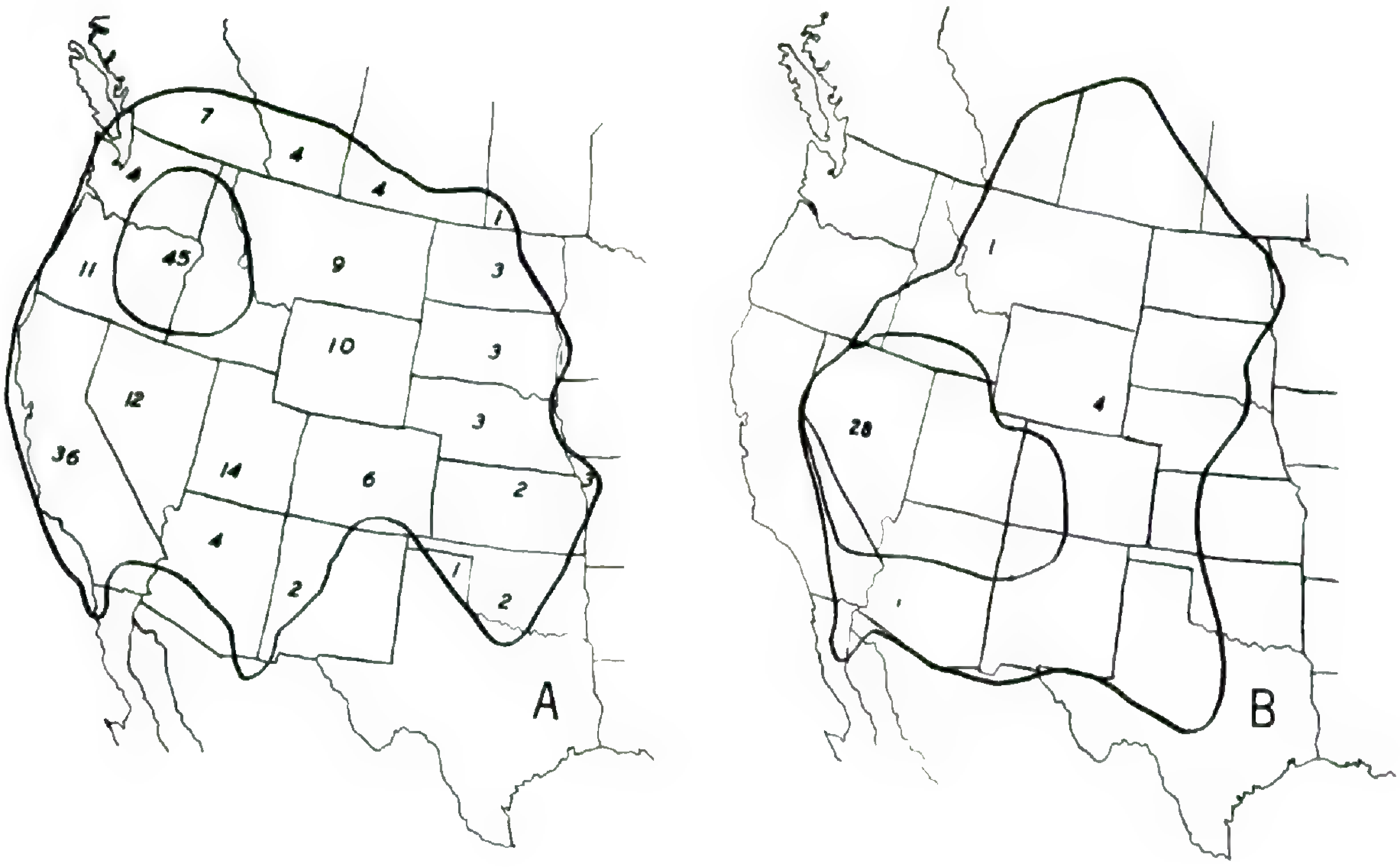
Of special interest art the 39 genera of *Apioideae* with over 200 species which are endemic to western North America. Two centers of distribution may be recognized for these genera; one in Pacific North America, including the Rocky Mountains, where 195 species are endemic, 31 extend into adjacent and equivalent areas,

and only 12 occur extensively in other areas; the second in extratropical Mexico and Central America with 133 endemic species, 23 extending into adjacent and equivalent areas and only two occurring extensively in other areas.

The largest genus in Pacific North America is *Lomatium* with 80 species. A major center for differentiation of this genus (Figure 9A) is in the grass and scrubland of western Washington, Oregon, and adjacent Idaho where over half of the species occur. *Lomatium* is represented in the California flora by 46 taxa, (species and varieties) 10 of which are endemic and show adaptation to such specialized habitats as serpentine outcrops, 19 occur in drier areas of the state associated with sagebrush (*Artemisia tridentata Nutt.*), chaparral, or desert woodland vegetations, and only 17 are in more mesic habitats. Most species of *Lomatium* flower in the early spring before summer drying occurs; they are perennial and may be considered well adapted to the summer dry regime since in drier areas the plants are completely dormant by the beginning of the summer dry season.

The other large endemic genus in Pacific North America, *Cymopterus,* is possibly a derivative of an *Angelica*-like stock which has become adapted to drier sites. Of the 32 species, 28 are found within the Great Basin and desert areas roughly bounded by the Snake River of Idaho, Sierra Nevada of California, Colorado River of Arizona, and the Rocky Mountains of Colorado (Fig. 9B). The species occur in desert areas but cannot be considered true desert plants but rather drought- or desert-evaders. They are deep-rooted perennials and are among the earliest plants to flower in the spring when they may even be found flowering along the edges of snowbanks. The desert species at low elevations occur commonly in sinks or basin areas where water collects seasonally. By early summer they are in mature fruit and the foliage withered. Even at higher elevations their fruiting is completed early in the season. Some years ago I had the opportunity to observe a population of *Cymopterus purpurascens* (Gray) Jones at 7300 feet elevation near the summit of Westgaard Pass, Inyo County, California, in mid-April when young fruit was already forming. On May 30 of the same year it was possible to locate the population only by a few dried leaf fragments and an occasional fruit.

The distribution of the Mexican highland and Central American genera may be exemplified by the genera *Prionosciadium, Rhodosciadium,* and *Donnellsmithia* (Fig. 10A) occurring in the mountains from Sonora and Chihuahua to northern Guatemala. Within this general area occur most of the Mexican genera of *Umbelliferae.* However, one fossil record of fruits from the Miocene Latah formation at Spokane, Washington (*Umbelliferospermum latahense*) has been tentatively described as a relative of the modern Mexican genus *Rhodosciadium* (Berry 1929) and is indicative of a much more extensive distribution for this group in the Tertiary. The present distribution of one Mexican highland genus, *Tauschia,* also indicates a wider range in the Tertiary since relict species of the genus occur from coastal Southern California to the northern Cascades in Washington (Fig. 10B). The genus *Arracacia* (Fig. 10C) shows a somewhat different pattern from that of *Prionosciadium* and *Tauschia,* extending for some distance south along the Andean chain and although doubtless of northern affinity and origin it would seem to be advancing into the southern hemisphere. One other taxon may be mentioned, the



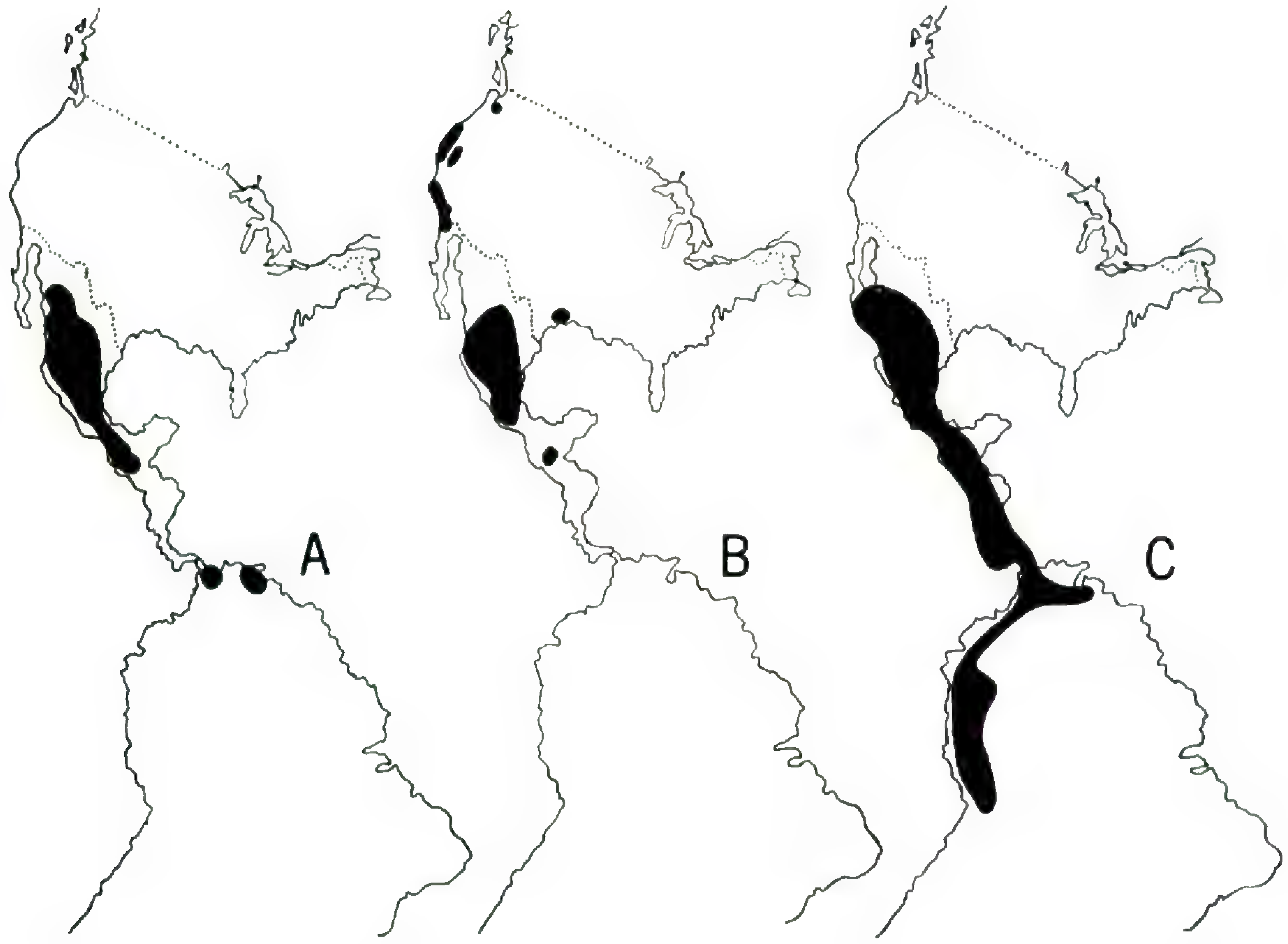


Fig. 9 (top). Distribution of the genera (A) *Lomatium* (80 species) and (B) *Cymopterus* (32 species) in western North America. Numbers indicate the number of species in each general area. Fig. 10 (bottom). Distribution of the genera (A) *Prionosciadium* (16 species), *Rhodosciadium* (13 species), and *Donnellsmithia* (13 species); (B) *Tauschia* (20 species); and *Arracacia* (25 species).

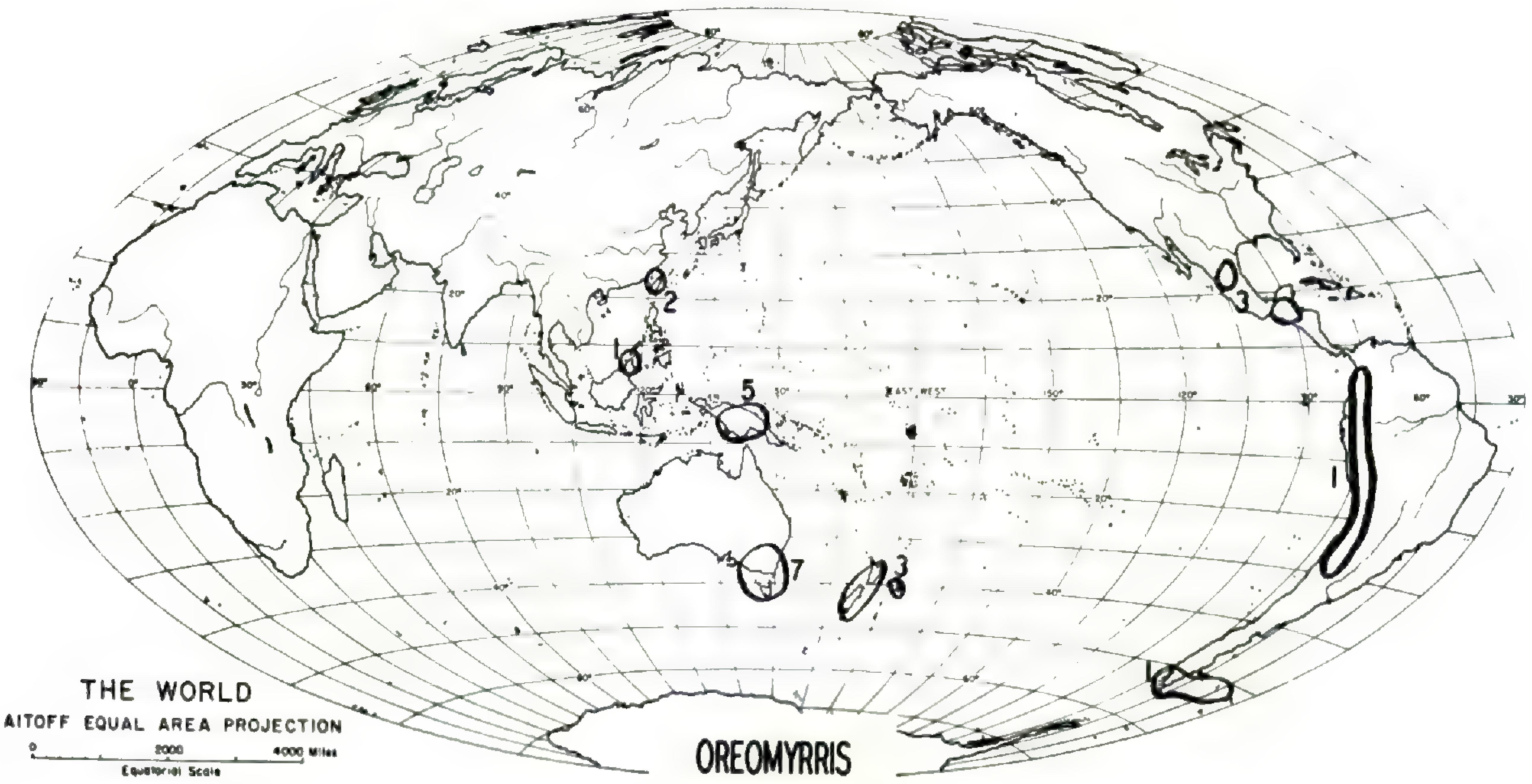


Fig. 11. Distribution of the genus *Oreomyrrhis* (23 species).

genus *Oreomyrrhis* (Fig. 11) which reaches southern Mexico. It is the only member of the subfamily *Apioideae* which occurs almost entirely in the southern hemisphere. Mathias & Constance (1955) have suggested that this genus may be a derivative of an Antarcto-Tertiary Geoflora. Its anomalous distribution is one of many unsolved geographical problems.

It is suggested by these patterns in western North America that with the differentiation of drier climates in the Pliocene certain elements of the widely ranging Umbelliferae became adapted to grasslands and desert borders and were components of the Madro-Tertiary Geoflora. The present Mexican genera may be the modern derivatives of this flora, only the genus *Tauschia* retaining sufficient variability to survive in more northern latitudes. The genera in western North America do not fit into one pattern of distribution but into several. There is still a large representation of Arcto-Tertiary derivatives occurring in mesic habitats, many of the genera essentially holarctic. *Angelica, Ligusticum, Osmorhiza,* and other genera mentioned earlier are in this category. There is a small group of probable relict genera surviving in mesic montane areas. These include *Podistera, Oreonana,* and *Oreoxis.* However the greatest differentiation seems to be occurring in the two groups of genera which became components of the Madro-Tertiary Geoflora, such as *Lomatium* and *Cymopterus* in the Great Basin and the many genera of Mexico and Central America.

The historical development of the family *Umbelliferae* cannot be determined from its fossil record. In North America there are no records prior to the Tertiary and fossil fruits have been described for only seven species in as many genera. Four of these are Pleistocene records referred to modern species (Table 1). Consequently the past history of the family must be inferred largely from a study of modern distributions and their correlation with those for other closely related groups, particularly the Araliaceae. It is suggested from this brief survey of the generalized distributions of a few genera of *Umbelliferae* and a comparison of the distribution of the entire family with that of the *Araliaceae* that the *Umbellales*

(sensu strictu) are an ancient tropical group, already differentiated into modern genera or their prototypes in the widely ranging Cretaceous floras of the world. The largely herbaceous *Umbelliferae* were presumably derived from a tropical woody pro-araliaceous stock in temperate environments probably at higher elevations. They expanded both north and south from the tropics and were differentiated, probably by late Cretaceous, into modern sub-families or their prototypes, *Hydrocotyloideae* in the south, *Saniculoideae* and *Apioideae* in the north. The present disjunct distributions for the western hemisphere representatives of the family are the result of climatic and topographic changes beginning in late Oligocene. They are not unique but they may be matched in other families (Axelrod, 1958). Certain of the north-south disjunctions may be the result of recent accidental dispersal or may represent mountain hopping along the Andean chain.

Some Antarcto-Tertiary derivatives of the family have expanded into temperate areas somewhat north of the equator and likewise Arcto-Tertiary derivatives have ranged into the tropics and southward at higher elevations. The primary center of differentiation for the present representatives of the *Umbelliferae* is in the dry climate of the Mediterranean area. A secondary center occurs in western North America. The differentiation and expansion of the family in these regions is apparently in response to progressively drier environments.

Table 1. Cenozoic Araliaceae and Umbelliferae of North America[1]

	Paleocene	*Eocene*	*Oligocene*	*Miocene*	*Pleistocene*
ARALIACEAE-ARALIEAE					
1. *Aralia alexoensis* Bell	Alberta				
2. *A. browni* Berry		Wyoming			
3. *A. browniana* Heer	Greenland				
4. *A. coloradensis* Knowlton	Colorado				
5. *A. dakotana* Knowlton &	British Colombia				
Cockerell	North Dakota	Mississippi			
		California			
6. *A. delicatula* Hollick		Alaska			
7. *A. dissecta* Lesquereux			Colorado		
8. *A.* (?) *gracilis* Lesquereux		Wyoming			
9. *A. hercules* (Unger) Saporta	Colorado				
10. *A. jörgenseni* Heer	Greenland	Mississippi			
11. *A. lasseniana* Lesquereux		California			
12. *A. lobata* Knowlton	Colorado				
13. *A. longipetiolata* Jennings			Montana		
14. *A. looziana* Saporta & Marion	Montana				
15. *A. notata* Lesquereux	Montana	British Columbia			
	Colorado	Oregon			
	Wyoming	Arkansas			
	North Dakota	Louisiana			
	Alberta	Texas			
	Saskatchewan				
16. *A. notata denticulata* Berry		Wyoming			
17. *A. reesidei* Knowlton	Colorado				
18. *A. republicensis* Brown			Washington		
19. *A. rubyensis* Becker			Montana		
20. *A.* (?) *semina* Berry		Kentucky			
21. *A.* (?) *serrata* Knowlton	Colorado				
	New Mexico				
22. *A. serrulata* Knowlton	Wyoming				

Table 1. Cenozoic Araliaceae and Umbelliferae of North America (*Continued*)

	Paleocene	*Eocene*	*Oligocene*	*Miocene*	*Pleistocene*
23. *A. taurinensis* (Ward) Sanborn	Montana Saskatchewan Alberta	Oregon Louisiana Kentucky Texas			
24. *A. triloba* Newberry	North Dakota Saskatchewan				
25. *A. wrightii* Knowlton				Wyoming	
26. *A. wyomingensis* Knowlton & Cockerell	Wyoming Colorado				
27. *A.* (?) sp. Hollick	Alaska	Alaska			
28. *A.* (?) sp. Hollick	Alaska	Alaska			
29. *A.* sp. Knowlton				Wyoming	
30. *A.* sp. Knowlton		Oregon			
31. *A.* (?) sp. Knowlton		Oregon			
32. *A.* (?) sp. Knowlton	Colorado				
33. *A.* sp. Lesquereux		Louisiana			
34. *Aralinium excellens* Platen		California			
35. *A. lindgreni* Platen		California			
36. *A. multiradiatum* Platen		California			
37. *A. parenchymaticum* Platen		California			
38. *Panax andrewsii* Cockerell			Colorado		
ARALIACEAE-SCHEFFLEREAE					
1. *Hedera auriculata* Heer	Alaska	Alaska			
2. *H. parvula* Ward	Montana				
3. *Oreopanax conditi* La Motte			Nevada		
4. *O. gigantea* (Knowlton) Arnold				Oregon Mississippi	
5. *O. minor* Berry		Tennessee			
6. *O. mississippiensis* Berry		Mississippi			
7. *O. oxfordensis* Berry		Arkansas Mississippi			
8. *O. precoccinea* (Brooks) Arnold				Oregon Idaho	
9. *O. wilcoxensis* Berry		Tennessee Texas			
10. *O. wilcoxensis crenulatus* Berry		Tennessee			
11. *O.* (?) sp. Bell	Alberta				
12. *Schefflera elliptica* Berry		Tennessee Kentucky			
13. *S. formosa* Berry		Tennessee Kentucky			
UMBELLIFERAE-APIOIDEAE					
1. *Cymopterus* (*Glehnia*) *littoralis* Gray					California
2. *Daucus pusillus* Michx.					California
3. *Oenanthe sarmentosa* Presl					California
4. *Oxypolis destructus* Cockerell			Colorado		
5. *Peucedanites nordenskiöldi* Heer	Greenland				
6. *Umbelliferospermum latahense* Berry				Washington	
7. *Zizia* sp. Brown					Louisiana

[1] Taken from Boureau, 1965-64; Knowlton, 1919; La Motte, 1944, 1952. No records for Pliocene.

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SOUTH AMERICAN LOBELIOIDEAE NEW TO SCIENCE

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The *Lobelioideae*—now usually regarded as a subfamily of the *Campanulaceae*, but formerly at least often treated as a distinct family, *Lobeliaceae*—comprise a natural taxon not easily confused with any other. As in many another "natural" family and subfamily, however, intra-familial taxa are often difficult to separate. According to the most recent revision of the *Lobelioideae*, that of the late F. E. Wimmer (Pflanzenreich **IV.** 276b, parts 1 and 2 [Hefte 106, 107] 1943, 1953), the group includes 29 genera and 1157 species well distributed throughout the world. About 70 percent of the species belong to three large genera: *Lobelia* (cosmopolitan, 383 species), *Centropogon* (chiefly South American, 226 species), *Siphocampylus* (Tropical American, 207 species). About 93 percent of all the species belong to one or another of ten genera; the next seven are, in order: *Burmeistera* (chiefly South American, 77); *Cyanea* (Hawaii, 60); *Pratia* (tropical, 34); *Clermontia* (Hawaii, 28); *Laurentia* (cosmopolitan, 25); *Lysipomia* (Andean, 19); *Monopsis* (African, 18). Looked at from the other end, there are 7 monotypic genera, and 9 genera with 2-8 species each. The unifying features of the *Lobelioideae* are in the corolla and androecium, which are so well known as to need no description here, and so nearly uniform throughout the subfamily that they provide in themselves scarcely any dependable taxonomic distinctions at the generic level. Most generic distinctions have been made on the basis of the fruit; e.g., whether a capsule or berry, whether (if a capsule) loculicidal or circumscissile, whether 1- or 2- locular, etc. Most of the smaller genera occupy limited geographical ranges and are also morphologically well set apart; e.g. *Dialypetalum* in Madagascar; *Phyllocharis* in New Guinea; *Apetahia* in Polynesia; *Legenere* and *Downingia* in Chile and in the Californian region; *Lysipomia* in Andean South America.

There are among the American *Lobelioideae* two classes of genera that do not fit neatly and logically into taxonomic systems. Such genera are either large and diverse but not readily divisible into subordinate taxa (e.g. *Lobelia, Siphocampylus, Centropogon*), or small in number of species but either too close to *Lobelia* or evidently genera of convenience only. *Diastatea,* for example, is a group of 5 or 6 species, chiefly Mexican. The plants are small annuals, distinguished by having the ovary superior or nearly so, the corolla not cleft to the base but distended by the expanding ovary. The genus seems to be a natural evolutionary unit, but it is not very different from *Lobelia.* Most (but not all!) Mexican species of *Lobelia* have an inferior ovary (as usual in the subfamily); most (but not all!) have the corolla cleft to the base; in the appropriately named *Lobelia diastateoides* the ovary is superior and distends the corolla, but the corolla-tube is cleft half its length, and the plant is perennial. The recognition of *Diastatea* as a genus, in other words,

ANN. MISSOURI BOT. GARD. **52**(3): 399-409. 1965.

depends upon a combination of features, none of which in itself is sufficient. Another small—and also chiefly Mexican—genus, *Heterotoma*, is apparently not a "natural" group like *Diastatea*, but a genus of convenience, based on the single feature of the gibbous or spurred base of the flower; this is discussed further on in this paper.

The species that are described below are based on specimens sent to me for identification from the Royal Botanic Gardens, Kew; from the United States National Herbarium; and from the University of California, Berkeley. Explorations in recent years have brought to light a number of novelties from the Eastern Cordillera of Colombia and from the mountains of southern Ecuador and northern Peru. It is increasingly evident that in the *Lobelioideae*, as in other plant-families, interpretation of the Andean floras depends upon an understanding of the possibilities for local endemism and the development of microspecies, and at the same time an understanding of the changes that may take place in species that are widely distributed along the Andes. Suffice it to say here that almost every mountain in the Andes seems to have different species on it, and no one except Wimmer has ever known the large genera well enough to be able to distinguish confidently between what is new and what is merely a variant of a species already known. The most difficult groups by far are *Burmeistera*, which is developed chiefly in Colombia and Ecuador, and the two largest groups of *Centropogon*, namely those species with branched hairs, and those with cornute anthers, respectively. Each of these latter groups is represented by numerous species from Bolivia to Central America; many are known from the types only, and the differences between them are often subjective. It is worth emphasizing, therefore, that although recent monographs by a competent specialist have treated the South American *Lobelioideae* in great detail, a host of new and puzzling things turn up in every new collection from the Andes, and it is apparent that there is still a lifetime of work for someone interested in the study of these bizarre and beautiful plants. Until we know more about the so-called species that have already been described, the limits of their variation and the differences between them, descriptions of individually aberrant specimens would seem to have little value. In the following paragraphs, therefore, I have limited myself to the description of a few extraordinary new taxa whose real relationships are in doubt.

Burmeistera **pteridioides** McVaugh, sp. nov., herbacea, minute puberula, foliis angustis, pinnatifidis, lobulis sublinearibus; hypanthium tam fere latum quam longum, basi rotundatum; calycis lobi erecti usque patentes, hypanthio breviores; flores solitari-axillares, 3 cm. longi, corollis ut in subsect. *Genuinae*. Fig. 1,A.

A weak herb ("straggling"), up to 1 m high, nearly glabrous, the leaves minutely puberulent beneath especially on the veins; leaves pinnatifid, the blades narrow in outline, 7-10 cm long, 1.5-3 cm wide, with 10-12 linear or tapering, entire, obtuse lobes on each side of the midvein; lobes 1.5 cm long or less, 1.5-2.5 mm wide at base, almost at right-angles to the central rachis (which is 2-3 mm wide), or arcuate-ascending; upper and lower lateral lobes shorter than the middle ones, the terminal

one linear, 1-1.5 mm wide, 2-3 cm long; petioles 2 mm long; flowers axillary to the upper leaves, the stout ebracteate pedicels up to 8-10 cm long in fruit; flowers 3 cm long; corolla "green, somewhat darker and purplish on the outside" (Grubb *et al.*), its tube 10 mm long, abruptly contracted above the base to an isthmus 2 mm in diam, thence enlarged to the mouth; lobes all strongly deflexed-falcate, the dorsal pair 12 mm long, 3 mm wide, the lateral ones 7 mm long, the ventral one 5 mm; filament-tube 22 mm long, pubescent; anther-tube 7 mm long, 2.5 mm in diam, flaring at the distal end, bearing a few yellow hairs near the base, and a few long hairs on the margins of the lower (ventral) anthers; hypanthium rounded at base, 4 mm high, 3 mm in diam; calyx-lobes bluntly triangular, 3 mm long, 2 mm wide at base, blunt-tipped, with 1-2 prominent teeth on each side; fruit inflated, apparently oblate, "bright pink with white pulp" when ripe, about 1.2 cm high, 1.7 cm in diam; seeds brown, compressed, elongated, unilaterally margined, 1.2 mm long.

COLOMBIA: BOYACA: Sierra Nevada de Cocuy, in cloud forest by path from Báchira to Borota, on ground and on a fallen tree, elev ca 2250 m, 21 Aug 1957, *P. J. Grubb et al. 652* (K, holotype).

Little is known of the biology of the Andean species of *Burmeistera,* as most of the species have been described by authors who have never been in the American tropics where the plants grow. Several species are known to have flowers and fruit much like those of *B. pteridioides,* and in fact in this group specific differentiation has been accomplished chiefly on the basis of leaf-characters and those of the calyx-lobes. I know of no instance in which forms with pinnatifid leaves occur in species having normally dentate leaves, so I venture to describe as a new species this plant from a previously little-explored area.

Centropogon **varicus** McVaugh, sp. nov., scandens, sparse pilis arbusculiformibus vestita; hypanthii tubus supra ovarium 2-3 mm productus, calycis lobis 3 dorsalibus in labium coalitis; antherarum 2 inferiores apice cornutae; folia elliptica, acuminata, denticulata, brevipetiolata; flores in axillis foliorum summorum, 7.5-8 cm longi, pedicellis 5-5.5 cm longis; calycis labium dorsale 5-7.5 mm longum, apicibus liberis 1-2 mm longis; corollae tubus 45-48 mm longus, rectus, basi constrictus; lobi falcato-deflexi; filamenta 60-70 mm longa, pubescentia. Fig. 1,B.

A scaberulent vine, climbing 2-6 m, the herbage soon glabrate, when young glutinous-pubescent with rusty-brown rigid sparingly branched hairs up to 0.5 mm long; leaves elliptic, 2-3 (-5) cm wide, 6-10 cm long, about 3 times as long as wide, slenderly acuminate, acute or somewhat rounded at base, callose-denticulate with purplish teeth; petioles 1-1.5 cm long; flowers 7.5-8 cm long, in the axils of the somewhat reduced upper leaves; pedicels 5-5.5 cm long, bibracteolate, the bracteoles 2 mm long or less, 5-12 mm above the base of the pedicel; corolla scabrous without, about 5 cm long, "scarlet" (*Wurdack,* no. *916*), or "salmon, the lobes yellow" (no. *928*); tube 45-48 mm long, narrowly funnelform, the narrow basal portion about 2 mm wide, the mouth 7-10 mm wide when pressed flat; lobes decurved-falcate, standing nearly at right-angles to the tube, the dorsal pair 20 mm long, 5 mm wide at base, the others about 10-12 mm long; filament-tube 60-70 mm long,

pale-pubescent; anther-tube "purple," 8 mm long, 3 mm in diam, sparingly stiff-pilose distally, the two shorter anthers cornute, the appendage of white concrescent hairs 4 mm long; hypanthium urceolate, rounded at base, 8-10 mm high, 5 mm in diam, prolonged 2-3 mm beyond the summit of the ovary; calyx 2-parted, the 3 dorsal lobes united into a broadly triangular, sparingly denticulate lip 5-7.5 mm

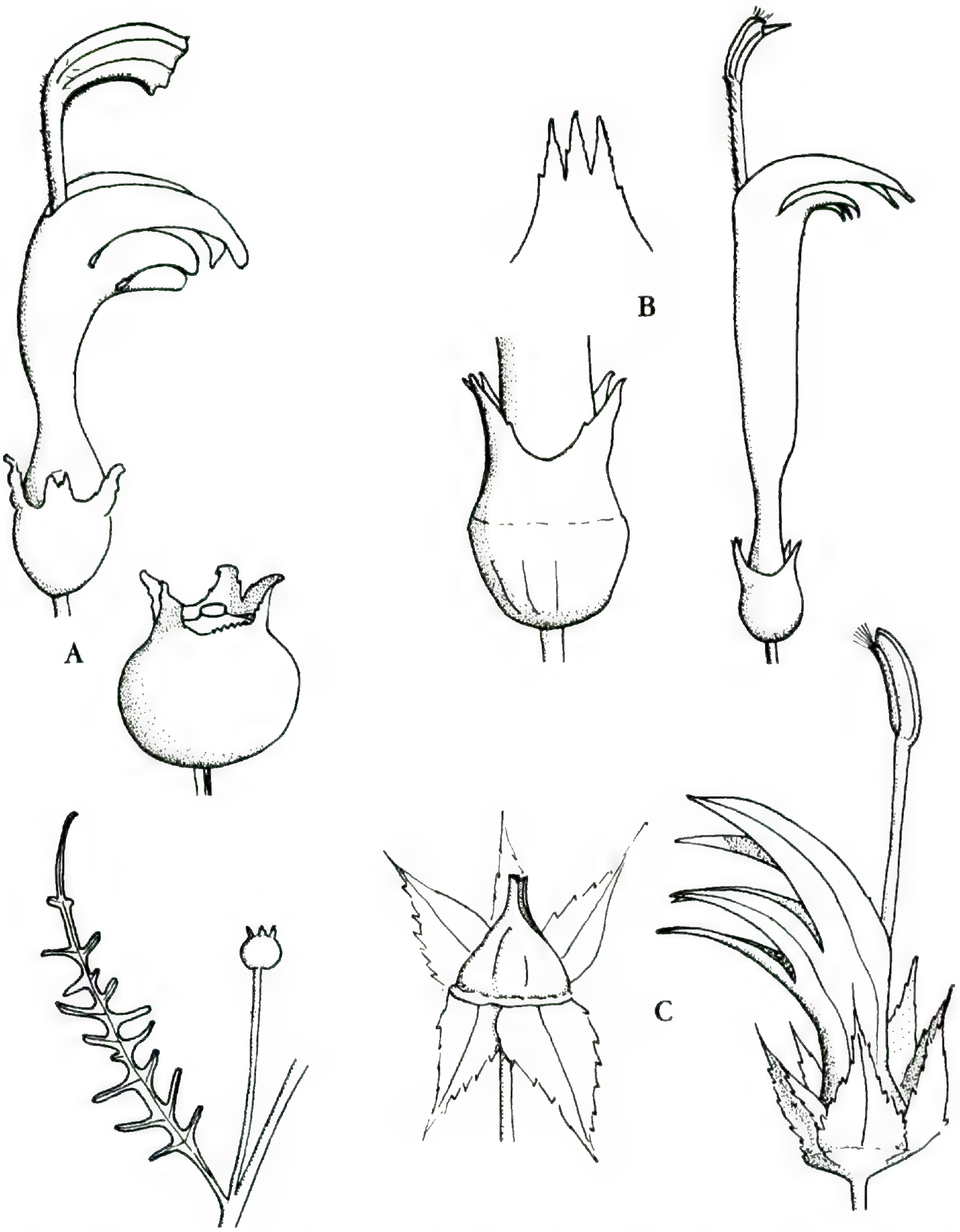

Fig. 1: A. *Burmeistera pteridioides* (holotype); flower, 2.5×; immature fruit, 2.5×; leaf and axillary pedicel, 0.5×. B. *Centropogon varicus* (holotype); dorsal lip of calyx, 2.5×; flowering calyx and hypanthium, 2.5×; flower, 1×. C. *Siphocampylus exuberans* (holotype): fruit showing apical dehiscence, 1×; flower, 1×.

long, 6-8 mm wide at base, the tips of the lobes free 1-2 (-3) mm; ventral lobes united into an opposing, similar but slightly smaller lip; mature fruit not seen, probably ellipsoid, ca 10 mm long, 6-8 mm wide; seeds ellipsoid, 0.7 mm long.

PERU: AMAZONAS: Prov Bongará, hills WNW (310°-320°) of Pomacocha, elev 2300-2700 m, frequent at moist forest edges, 19 June 1962, *J. J. Wurdack 916* (MICH, holotype); same locality and date, *Wurdack 928* (MICH).

Students of the *Lobelioideae* have often noted that a long straight corolla with decurved-falcate lobes may be found in species of several different sections of *Centropogon;* that is, the form of the corolla is not in itself diagnostic. It has always been assumed, however, that the rather large group of species with cornute anthers (i.e. Sect. *Centropogon*, by almost all authors called *Eucentropogon*) constituted a natural section, and that another large group with penicillate anthers and pubescence of branched hairs (i.e., Sect. *Siphocampyloides*, subsect. *Brevilimbati;* see Brittonia **6:** 459. 1948), was equally natural and homogeneous. Now in *Centropogon varicus* [*varicus*, straddling] is described for the first time a species combining the cornute anthers (and the basally connate calyx-lobes of some species) of Sect. *Centropogon* with the arbusculiform hairs of Subsect. *Brevilimbati.* This combination of characters, and the bilabiate calyx (itself unique as far as I know) make *C. varicus* one of the most distinctive species in the genus.

Siphocampylus **exuberans** McVaugh, sp. nov., glabra, folis ovatis, cordatis, acuminatis, fimbriatulato-dentatis; flores solitarii in axillis foliorum superiorum, pedicellis flexuosis bibracteolatis 6-8 cm longis; corolla 4.5 cm longa, eius tubo 2-2.3 cm longo, limbo breviori; lobi corollae gradatim profundius soluti; filamenta 40-50 mm longa, antherae 10-13 mm longae; hypanthium breve, ovarium fere superum, calycis lobi foliacei, patentes, 1.5-2 cm longi, 1 cm lati, prominenter fimbriato-dentati. Fig. 1,C.

Glabrous "climber" to 4.5 m long; leaves ovate, scabrous above, cordate, slenderly acuminate, fimbriatulate-dentate with pale slender callose teeth 1 mm long; blades 2.5-4.5 cm wide, 6-9 cm long, on flexuous petioles 1.5-2.5 cm long; acumen 1.5-3 cm long; flowers 5-6 cm long, in the axils of the principal leaves, on stout flexuous bibracteolate pedicels 6-8 cm long (in fruit); corolla 4.5 cm long, "dull yellow with purple veins & patches, lobes pinkish" (according to the collectors); tube 2-2.3 cm long, narrowed from both ends to the middle, where 6-8 mm wide when pressed flat; lobes all somewhat recurved-falcate, the dorsal pair 25 mm long, 7-7.5 mm wide at base, the lateral and ventral lobes similar but successively shorter; filament-tube 40-50 mm long; anther-tube 10-13 mm long, 3 mm in diameter, gray, glabrous, but the two short anthers copiously white-tufted at apex; hypanthium shallow, nearly flat in anthesis, the ovary essentially superior; calyx-lobes foliaceous, similar in shape to the leaves and similarly dentate, 1.5-2.5 cm long, 1 cm wide including the teeth, in flower stellately spreading, in fruit more or less reflexed; capsule superior, conic, about 1.5 cm wide at base, 1.2 cm high, beaked 4 mm by the persistent style-base; seeds oblong, compressed, pale-tipped, 1.3-1.5 mm long.

ECUADOR: NAPO-PASTAZA: Oriente trail ENE of Cayambe Mountain, in dwarf forest, elev 3000 m ["10,000 ft."], "10.12" 1961, *P.C.D. Cazalet* & *T. D. Pennington 5563* (MICH, holotype; K, US, isotypes).

Because of its large yellowish corolla with relatively long lobes and short tube, and because of its long filaments, this species would ordinarily be referred to the subsection *Megastomi* (cf. Pflanzenreich **IV.** 276b, part 2 [Heft 107]: 266. 1953). On the basis of plant-habit and flower-morphology in general, however, I believe it finds its closest affinity with a small group of species called by Wimmer the *Elegantes* (Pflanzenreich, p. 304). The latter are characterized by their flat or flattish hypanthium and essentially superior ovary and by their often foliaceous, toothed and spreading or reflexed calyx-lobes. In most of the *Elegantes*, however, the calyx-lobes are narrower than those of *S. exuberans*, the corolla-tube is narrower and straighter, and the leaves are less prominently toothed and seldom cordate.

Lobelia **heteroclita** McVaugh, sp. nov., herbacea, stricta, supra hispidula, foliis ellipticis, crenato-dentatis, subsessilibus; racemis longis, 100-150-floris, floribus tenuiter pedicellatis, floratione invertis, 4.5 cm longis; corollis puniceis fenestratis, unilabiatis; hypanthio gibbo, calycis lobis duobus ventralibus oblique divergentibus; filamentis 35-38 mm longis, basi inter se liberis 10-12 mm, dorsalibus 3 glabris, ventralibus 2 pubescentibus, in calcar productis. Fig. 2,A.

Herb 1.5 m high, probably simple and strict, the stem more than 1 cm in diam at base; upper stem, pedicels and hypanthia hispidulous; leaves [those of the basal half of the stem not seen] elliptic, or the lower [probably] oblanceolate, 2-4.5 cm wide, 7-10 cm long, 2-3 times as long as wide, crenate-dentate, acute or obscurely acuminate, rounded or abruptly contracted to a nearly sessile base, glabrous and lustrous above, glabrous beneath except for scattered colorless hollow flaccid hairs 1-1.5 mm long; inflorescence a leafy-bracted spikelike raceme 30-60 cm long, the lower bracts leafy, the upper ones gradually reduced in size; flowers 100-150, on short-hirsutulous ascending slender pedicels 1.5-2 cm long, these bibracteolate near base; flowers inverted in anthesis, 4.5 cm long; corolla "deep pink" (according to Grubb *et al.*), slender, 6-7 mm wide at base when pressed flat; tube 36-38 mm long, cleft dorsally to the base, fenestrate 10-12 mm at base, straight, gradually tapering from base to near apex (to about 2.5-3 mm wide), then curved abruptly toward the ventral side and contracted to the base of the lobes, where 2 mm wide or less; limb scarcely bilabiate, the lobes long and narrow, the dorsal ones 9-12 mm long, 1.5 mm wide, slightly longer than the 3 ventral, all declined in a group at an angle of about 45° with the narrow portion of the tube; filament tube 35-38 mm long, glabrous, the filaments distinct at base for 10-12 mm, the 3 dorsal ones glabrous, the two ventral ones pubescent like the ovary, extending into the gibbous prolongation of the calyx; anthers 4.5 mm long, slate-gray, the two ventral ones white-tufted at apex; hypanthium shallow, obliquely gibbous ventrally, the two ventral calyx-lobes somewhat directed outward; lobes triangular, 8-9 mm long, 2 mm wide at base, slender-pointed, entire or obscurely denticulate; ovary bilocular; seeds numerous on two axile placentae, not seen mature.

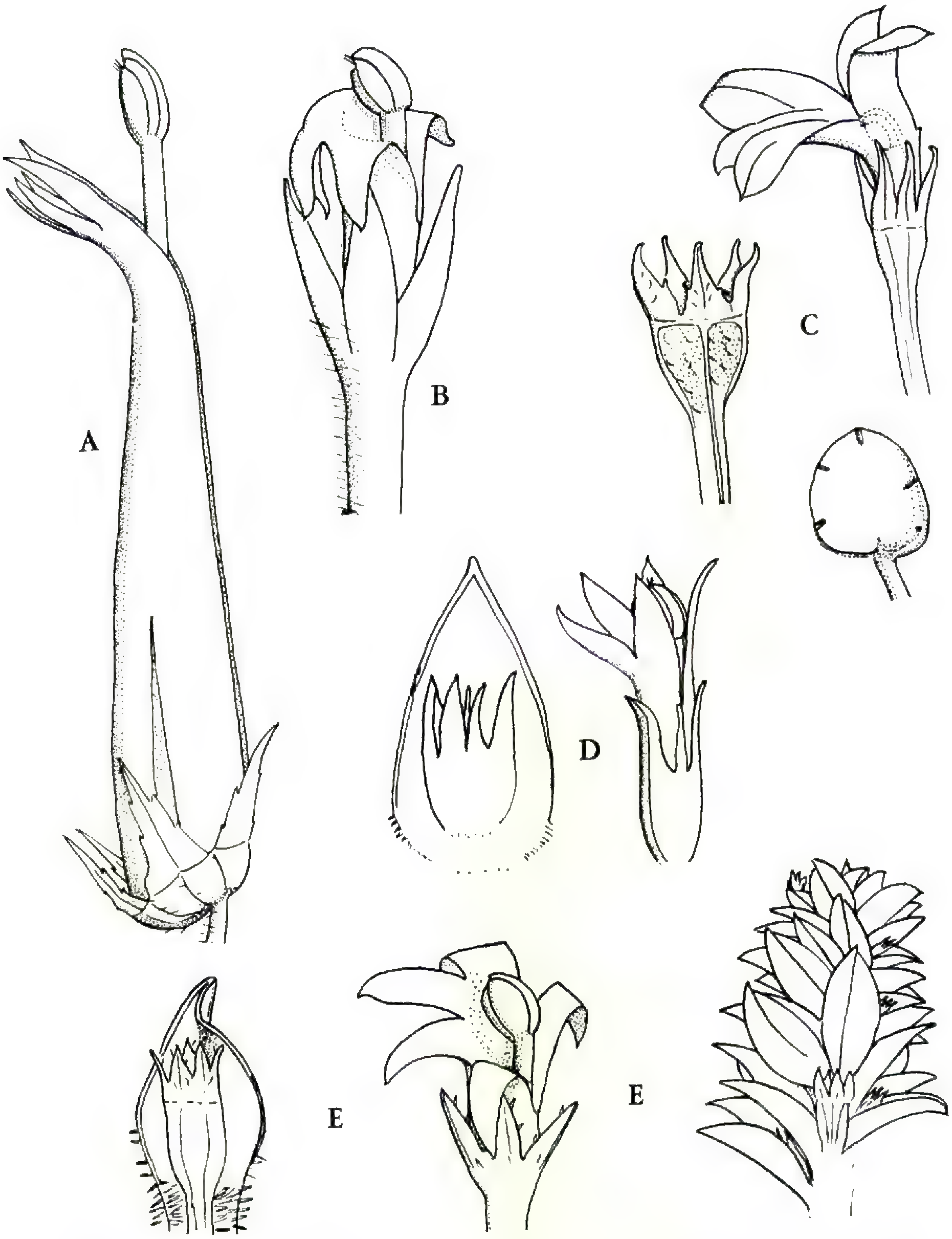

Fig. 2: A. *Lobelia heteroclita* (holotype); flower, 2.5×. B. *Lysipomia muscoides* subsp. *delicatula* (holotype); flower, 12.5×. C. *Lysipomia subpeltata* (holotype); flower, 5×; mature fruit, 5×; leaf, 5×. *D. Lysipomia hutchisonii* (holotype); detached leaf with sessile axillary fruit adherent at base to the adaxial surface, 5×; flower, dorso-lateral view, showing the small dorsal calyx-lobe, 5×. E. *Lysipomia wurdackii* (holotype); detached leaf with axillary fruit adherent at base to the adaxial surface, 5×; flower, 10×; leafy branchlet, 2.5×.

Colombia: boyaca: Sierra Nevada de Cocuy, Laguna Seca, in more or less cleared area of cloud forest, elev ca 2750 m, 18 Aug 1957, *P. J. Grubb et al. 599* (US, holotype; K, isotype).

This extraordinary plant is apparently referable to the subgenus *Tupa* as delimited by Wimmer (Pflanzenreich **IV.** 276b, part 2 [Heft 107]: 409. 1953). The corolla is unilabiate (as understood by Wimmer), all the lobes essentially alike and declined in a single group. The American species of *Tupa,* however, are all either West Indian, Chilean, or natives of southern Brazil and the Argentine. No species has been known hitherto from the northern Andes. In *Lobelia heteroclita* the habit, the form of the inflorescence, and the form of the corolla suggest some of the Chilean and Brazilian species. As far as I know, however, *L. heteroclita* is unique among its supposed relatives in its gibbous hypanthium and the concomitant changes in the calyx and stamens. The development of a spur or gibbosity on the ventral side of the calyx and hypanthium has apparently taken place several times in the *Lobelia*-complex, as e.g. among the species of subgenus *Mezleria,* of the Southern Hemisphere (cf. Plazenreich **IV.** 276b, part 2: 600. 1953), and among the North American species referred to *Heterotoma* (cf. N. Amer. Flora **32A:** 31. 1943). The latter is surely a genus of convenience, as shown by the inclusion in it of such diverse species as *H. lobelioides* Zucc., with red and yellow flowers suggesting those of *Lobelia laxiflora* H.B.K., and on the other hand species with small blue flowers suggesting those of many Mexican species of *Lobelia,* sect. *Hemipogon.* I do not believe taxonomy would be well served by the addition to *Heterotoma* of a new element, a species apparently derived from yet another assemblage in the vast complex of *Lobelia.*

Lysipomia muscoides Hook. f. subsp. **delicatula** McVaugh, subsp. nov. A subsp. *muscoidei* floribus majoribus, foliis angustioribus; a subsp. *simulante* calycis lobis foliisque angustioribus, pubescentia densiori, differt. Fig. 2,B.

Tufted mosslike perennials, the leaves numerous and crowded in rosettes on a multicipital caudex; leaves narrowly linear-acicular, 5-6 mm long, about 0.4 mm wide at base, tapering to the blunt, gland-tipped apex, the distal half strongly outcurved or even recurved in the older leaves; blades entire, concave on the adaxial surface, convex on the abaxial, glabrous distally, copiously and coarsely ciliate from the middle or a little above this to the base, especially on the margins and the abaxial surface; flowers sessile or essentially so in anthesis and in fruit, 5 mm long including the thick stipelike base of the ovary; corolla white (*Wurdack*), scarcely bilabiate, the lobes flaring, triangular, about 1.5 mm long, 0.7 mm wide, ovate, acute; tube 2 mm long (1 mm long to the dorsal sinus); filaments 2 mm long; anther tube plump, purple-brown (Wurdack), 1.3 mm long, the shorter anthers cornute with 2 minute hyaline processes; hypanthium densely and coarsely ciliate with hairs like those of the leaf-bases, the calyx-lobes glabrous unless at the very base; fruiting hypanthium linear or somewhat expanded distally, 2-2.5 mm long, 10-ribbed, unilocular, the tube prolonged 0.7-0.8 mm beyond the summit of the ovary, the ovules on one linear longitudinal parietal (ventral) placenta; calyx-lobes narrowly triangular, entire, 1.5 mm long, more or less equal in size and shape, the

dorsal one usually a little larger, 2 mm long; seeds 10-15 or fewer, plumply ellipsoid, 0.6-0.7 mm long, finely and irregularly wrinkled.

PERU: AMAZONAS: Prov Chachapoyas, middle eastern Calla-Calla slopes, nr kms 416-419 of Leimebamba-Balsas road, elev 2900-3100 m, 9 July 1962, occasional on steep banks, *J. J. Wurdack 1286* (MICH, type); same locality, kms 409-410, elev 3100 m, 14 Oct 1964, *Hutchison & Wright 6940A* (UC).

In habit this plant is very like *Lysipomia muscoides* subsp. *muscoides*, of central Colombia, and subsp. *simulans*, of northern Colombia. From both of these it differs conspicuously in having narrow tapering leaves and a relatively luxuriant covering of stiff hyaline hairs on the leaf-bases and the hypanthia. Vegetative differences of a like order of magnitude are known among the local populations of other Andean species of *Lysipomia* (e.g. *L. spagnophila* Griseb., *L. laciniata* A. DC.); this suggests that the plant described here represents not a new species but another example of a localized race of a wide-ranging species.

Lysipomia **subpeltata** McVaugh, sp. nov., glabra, scaposa, foliis radicalibus, aggregatis, petiolatis, late ovatis, subpeltatis, 1-3 mm longis; scapis 2-4.5 cm longis; corollis 6-7 mm longis, roseis, labio inferiore basi croceo, purpureo-maculato; filamentis 2 mm longis. Fig. 2,C.

Glabrous scapose herb from an upright rootstock 4 mm long or less, bearing among the leaf-bases relatively thick adventitious roots 1-1.5 cm long, 0.7 mm thick; leaves 10 or more, on delicate slender petioles 2-3 mm long, "purplish, apparently peltate, hugging the ground" (Hutchison); blades up to 3 mm long and almost as wide, broadly ovate-cordate, standing at right-angles to the petiole which is inserted immediately distad of the basal sinus; margins seeming entire, but bearing 1-3 short peglike callose teeth on each side, the teeth abruptly infolded and appressed to the ventral surface of the blade; scapes (pedicels) 2-4.5 cm long, 0.5 mm in diam. ebracteate, prominently 5-angled below the flower; flowers 6 mm long (from the base of the hypanthium to the tips of the dorsal lobes of the corolla), the corolla "pale pink" (Wurdack), or "white with pink to lavender tints, lavender on outside" (Hutchison), the base of the lower lip yellow within and spotted dark purplish red; tube about 2 mm long to both lateral and dorsal sinuses, the latter bearing a small tooth; dorsal lobes outcurved, about 3.5 mm long, 1.3 mm wide; lower lip of corolla 4.5-5 mm long, the lobes 3.5 mm long, 1.8 mm wide; filament tube 2 mm long; anther tube plump, incurved, 1 mm long, the short anthers minutely appendaged; hypanthium campanulate, tapering into the pedicel, about 2 mm long in fruit; calyx lobes scarcely united at base, triangular, acute, about 2 mm long, 1 mm wide at base, the dorsal one slightly the longest, each lobe usually with 1 callose tooth on each side near base; ovary imperfectly bilocular; ovules probably about 50, on the two sides of the placenta which divides the basal part of the ovary; seeds ovoid, 0.7 mm long, minutely tuberculate in longitudinal lines.

PERU: AMAZONAS: Prov Chachapoyas, Cerros Calla Calla 19 km above Leimebamba, road to Balsas, on loamy slopes slightly raised above a bog, elev 3100 m, 14 Oct 1964, *P. C. Hutchison & J. K. Wright 6951* (MICH, holotype); same locality, but nr kms 411-416 of Leimebamba—Balsas road, 3100-3250 m, locally frequent on moist sandy bank, 11 July 1962, *J. J. Wurdack 1330* (MICH).

Few species of *Lysipomia* have the scapose habit and long-pedicellate flowers of *L. subpeltata,* and of these none has the broad subpeltate leaves nor the uniquely infolded marginal teeth. Presumably the nearest relative of *L. subpeltata* is *L. gracilis* (Wimmer) Wimmer, a poorly known species also from northern Peru. In *L. gracilis* the flower is about twice as large as that of *L. subpeltata,* and the leaves are narrow, crenate, and dilated at base.

Lysipomia **hutchisonii** McVaugh, sp. nov. Plantula caulescens caespitosa, consistens e ramulis carnosulis globularibus vel paullo elongatis, foliis multifariis rigidis carnosiusculis subtriangularibus acutis dense rosulatis; flores sessiles glabri; calycis lobi inaequales, lateralibus majoribus; filamenta 3.5 mm longa; corolla 6 mm longa; a *L. globulari* foliis subtriangularibus, calycibus glabris, differt. Fig, 2,D.

Caespitose, essentially glabrous, forming little mounds up to 10 cm or more across, with up to 25-30 short fleshy branches 1-3 cm long and 1-2 cm thick including the many-ranked leaves; roots adventitious, 1 mm thick or less, in a basal tuft; leaves about 15- to 20-ranked, closely imbricated, fleshy, rigid, ascending-spreading, about 100-200 clothing the tip of each branch in addition to the persistent dried ones below; blades sessile, entire, ovate-triangular, acute and short-cuspidate, 5-7 mm long, 3-4.5 mm wide at the widest part just above the base, glabrous except the minutely ciliate base; margins with narrow vitreous rim distally, the surfaces also glassy-lustrous; flowers sessile; corolla about 6 mm long, white (according to Hutchison), the slightly funnelform tube 3 mm long (about 1.3 mm long to the dorsal sinus); limb scarcely bilabiate, the lobes all a little outcurved, the dorsal ones slightly longer and narrower than the others, about 2.5 mm long and 1 mm wide; filament tube 3.5 mm long, adnate to the base of the corolla about 0.5 mm; anther-tube plump, about 1.5 mm long, apparently purplish-black, a little incurved, the two shorter anthers cornute with hyaline processes 0.3 mm long; hypanthium tangentially compressed, acute on the lateral margins, 2 mm wide in flower, after drying 2.5 mm wide in fruit, 2 mm long; calyx-tube prolonged 0.5 mm or less beyond the rim of the hypanthium; calyx-lobes narrowly triangular, entire (or often with a single glandlike tooth on one or both sides at the extreme base), acute or somewhat attenuate, 2-3 mm long, up to more than 1 mm wide at base; dorsal lobe usually, and one ventral lobe often, much smaller than the lateral ones, 0.2-0.5 mm wide, 1-1.5 mm long; operculum campanulate or slightly elongate, about 1.5 mm high; ovary unilocular, with about 20 ovules on one parietal placenta; seeds about 10, chestnut brown, ovoid, 0.7-0.9 mm long, minutely longitudinally striate.

PERU: AMAZONAS: Prov Chachapoyas, Cerros Calla Calla, 19 km above Leimebamba, road to Balsas, km 409-410, elev 3100 m, 14 Oct 1964, *Paul C. Hutchison* & *J. Kenneth Wright 6940* (MICH, type; UC, isotype); same locality, but 18 km above Leimebamba, steep places in sandy soil, very local, elev 3100 m, 8 June 1964, *Hutchison & Wright 5604* (MICH).

This species is very like *Lysipomia globularis* Wimmer, Field Mus. Publ. Bot. **13**(6): 485. 1937, but in the latter the leaves are linear or nearly so, and hardly more than 1.5 mm wide at base; the calyx-lobes are all fimbriate-ciliate except at the very tips, and the dorsal lobe (1.7-2.2 mm long) is longer than the others. The

two known collections of *L. globularis* came from Cutervo, Departmento de Cajamarca, Peru, a locality not far from that of *L. hutchisonii* but effectively separated from it by the valley of the Río Marañón.

Lysipomia **wurdackii** McVaugh, sp. nov., perennis, subglaber, caulescens, foliis conduplicatis pro genere latissimis 3-5 mm latis, floribus subsessilibus, filamentis 1.5 mm longis. Fig. 2,E.

Perennial, glabrous except the calyx-lobes and leaf-bases, with thick, apparently procumbent, sparingly branched stems 2-4 mm thick, up to 15 cm long, the basal portions bearing the remains of old leaf-bases, the tips 1-1.5 cm in diam including the closely imbricated many-ranked spreading conduplicate leaves; leaves spatulate, obovate or elliptic, concealing the upper stem, ciliate at base with stiff hyaline hairs up to 0.3 mm long, and sparingly beset with similar hairs on the adaxial surface at base; blades 6-8 mm long, 3-5 mm wide, keeled, obtuse, or the glandular apex forming an acute point; base broad, sessile; distal half of the blade with thick glassy margins, the surfaces also glassy-lustrous; flowers nearly sessile, somewhat enfolded by the subtending leaves, about 5 mm long including a stout pedicel-like base adherent to the leaf-base; corolla white (Wurdack), about 3.5 mm long, scarcely bilabiate, the lobes flaring, ovate, acute, nearly equal in size and shape, the two dorsal ones a little the longest, 1.7 mm long, 0.8 mm wide at base; tube about 2 mm long (1 mm long to the dorsal sinus); filament tube 1.5 mm long; anther-tube plump, 1 mm long, incurved, the two shorter anthers unappendaged; hypanthium somewhat tangentially flattened, in fruit 2 mm long, its tube prolonged about 0.5 mm beyond the summit of the ovary; calyx-lobes triangular, sparingly ciliate, nearly equal, 1.1-1.3 mm long, the dorsal one a little the longest; ovary unilocular; ovules and seeds about 20, on one longitudinal parietal (ventral) placenta; mature seeds irregularly ovoid, 0.6-0.9 mm long, tuberculate in longitudinal lines.

PERU: AMAZONAS: Prov Chachapoyas, summit of Cerro Malcabal (Cerro Tumbe), 3-6 km S.W. of Molinopampa, elev 2850-2900 m, 20 July 1962, occasional, *J. J. Wurdack 1416* (MICH, holotype).

The combination of long, stout branches, broad imbricate conduplicate leaves, and small sessile flowers, effectively distinguishes this newly described species from all others in the genus.

EXPERIMENTAL STUDIES ON SEEDLING DEVELOPMENT OF CERRADO WOODY PLANTS

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Abstract

Views of several authors concerning the natural regeneration of the cerrado (Brazilian wooded savanna) are summarized. Except for one, all of them agree that seed germination and seedling growth are disturbed by the harsh environmental conditions that prevail in the savanna. Unfavorable factors that have to be taken into account are dryness at soil surface, rather long drought period, and, above all, fire. Vegetative reproduction, on the other hand, is pointed out by the same writers as the most common means of maintenance and spread of the cerrado; the extent to which the plants set offspring vegetatively seems to be closely related to the degree of disturbance wrought in the cerrado environment by the factors mentioned above. For the study reported in this paper, many plants were grown in Rio de Janeiro (rain forest) zone) and at Paraopeba (cerrado zone), and observed from seed germination. A number of mature trees were also kept under observation in a small cerrado stand located in the Botantical Garden of Rio de Janeiro. A large number of data dealing primarily with seedling development is tabulated, with special reference to the length attained by both the primary root and the shoot at various ages. Data are also included which elucidate the germination features. Evidence is presented which indicates that, up to an age of two years, no taproot succeeds in reaching a depth of 1m. Thus the plantlets are forced to pass through 1-2 drought periods with their roots in the driest portion of the soil. It is recalled that in dry, sunny stations the cell walls are far more lignified and suberized in shoots and roots, and that the root cap cell walls are endowed with pectin, whose water-retaining ability is well-known. Accordingly, the suggestion is made that the real critical period in the establishment of seedlings in dry places is, as a matter of fact, the very early stages of development, when the cell wall devices have not had time yet to attain the necessary degree of completeness. It is suggested that many woody species peculiar to the cerrados would make their best growth if they received some additional water; this seems to mean that the seedlings would require favorable sites to become established in nature, where human disturbance and drought conditions are reduced to a minimum. However, this point must await fresh data from various sources. It has been verified that a number of seedlings can bear the destruction of either the primary root or the shoot; provided they are sufficiently watered, they soon remake the lost parts. Epigeal germination, which is mostly observed in trees, prevails largely over hypogeal germination; this in turn occurs primarily in undershrubs. A number of stowing tissues from underground tuberized organs were analysed for their water content; it ranged from 44 to 91% according to the ligneous or fleshly nature of the parts involved. The role of fire as a destructive agent for both seeds and seedlings is emphasized; insect larvae are also mentioned in this connection.

Introduction

Ferri (1961a) states boldly that: "after many years of studies in cerrados we were struck by the fact that we never found seedlings of permanent plants that we could say with certainty had come from seeds. Vegetative reproduction of various kinds is responsible for the maintenance of this vegetation in a certain place and for its spreading." Ferri (ib.) says further: "Experiments with seeds of *Stryphnodendron adstringens, Dimorphandra mollis, Bombax gracilipes, Kielmeyera coriacea, Annona coriacea, Aspidosperma tomentosum*, etc., have shown that there are no problems for the germination under laboratory conditions. However, the same seeds

Ann. Missouri Bot. Gard. **52**(3): 410-426. 1965.

sown in the cerrado germinate very poorly if at all. And even when some germination occurred the final survival of seedlings was extremely low." In another paper (Ferri, 1961b), he states again: "In the well-established cerrados I have never found plantlets of which I could say with certainty that they had come from seeds." Rizzini & Heringer (1962a) claim that: "It is through extensive suckering that the cerrado dwellers manage to survive the *disturbances wrought in their habitats by man,* and even to spread out over newly opened areas. Seeds play an insignificant part in this process, since the conditions existing there bring about serious difficulties to germination as well as keep the seedlings from growing *in most cases.* The great powers of vegetative reproduction those species prove to have account for their *resistance to fire and axe* under the well-known stunted condition." They refer to: "one experiment carried out by the authors at Paraopeba (which) shows that the cerrado plants are in need of more water to develop from seed than they receive from natural sources." This experiment consisted in sowing seeds of *Caryocar brasiliense* Camb. (Piqui) in cerrado soil with, as well as without, irrigation; for the next 10 months, irrigated seeds germinated freely, and seedling growth was excellent. Their concluding statement is as follows: "In fact, the savannas referred to display seed-born young plants only in especially favorable spots, where some moist, shaded depression exists."

Accordingly, the same investigators (ib.) record an instance of seedlings developing spontaneously when they write in reference to *Stryphnodendron barbatimao* Mart. ". . . however, we succeeded in finding young plants of various ages in nature." Some other instances have been found more recently of young plants from seed growing in protected sites in the cerrado. It should be noted that Rizzini & Heringer (ib.) insist on the fact, of great moment, that: "underground structures for vegetative propagation are also very peculiar to the *disturbed* savanna vegetation." Again: ". . . as for the regeneration out of seeds at later ages—this mainly in the usual *heavily disturbed status.* It is notorious that the putting in action of such a process depends especially upon *trauma.*"

It is quite evident that the more disturbed a cerrado is, the more intense is the vegetative reproduction it displays. Well-grown cerrados, and *cerradões* (forests made up of characteristic cerrado species bearing straight trunks), as recognized by a number of workers, constitute a *mesic environment* in which seeds do germinate and seedling growth takes place rather abundantly. In another paper the same authors (1962b) while referring to the shrubby storey in the *cerradão,* state that: "There is a large number of young plants produced by the extant trees."

Labouriau *et al.* (1963) assembled some data which seem at first sight to indicate that germination, and seedling growth, do take place normally in the cerrados. But one cannot avoid pointing out that the instances reported by them are too meager to clarify the issue involved in the natural regeneration of the Brazilian savanna, and that the cerrado in which their observations were carried out was well-developed showing a dense ground cover of herbs and shrubs; this keeps the soil surface in good condition of shelter for germination. In this connection, it is to be noted that the germinating seeds and plantlets *(Dalbergia violacea, Caryocar brasiliense,* and *Aspidosperma verbascifolium)* of Labouriau and his

co-workers were located "around a big tree" and "under a big tree," viz., at sheltered spots. The month, February, was, too, one of the most favorable ones since it is situated farther in the rainy season.

More recently, Rizzini (1964) has again commented on the point asserting

Fig. 1 (top). Closed, preserved cerrado at Varzea da Palma (Minas Gerais). Note the crooked treelets and the low grass cover. Photographed at the end of the rainy period. Fig. 2 (bottom). Open, touched cerrado at Varzea da Palma (Minas Gerais). Besides the crooked, small trees, note the grass cover taller than in Fig. 1. Photographed at the end of the rainy period.

once more that new plants arisen from seed are found but rarely in the cerrados.

L. Osse (1964), in devising a scheme designed to the recovery of extensive cerradoes for charcoal production, considered their regeneration by means of vegetative reproduction through gemmiferous roots as the sole workable one. He did not rely upon seeds, as he declares plainly. His standpoint may be instanced as follows (version): "In fact, the likelihood that a seed will come to germinate, and that the resulting seedling will grow up to be a tree, has been looked on as far scant in view of the environmental harshness, though highly tolerant species have been taken into account."

Among the earlier authors who treated this issue, Warming (1892) remarked that: "seeds, fruits, and young small plants are very easily destroyed by fire or killed by heat." But further on (ib.) he postulated that while seed-born herbs are seldom found in the cerrado, the major part of the adult trees come from seed. Finally, it must be recalled that, according to Warming (ib.), as early as 1835, Lund regarded propagation by seed in the cerrados as a mere exception.

Still more important in any case is to verify whether the plantlets originating from seed will in fact become established in the habitat *to a significant extent;* that a few of them succeed in doing so, the present writer, and others, have ascertained.

As neither of these discrepant views may be looked upon as a definitely acceptable explanation, it will generally be agreed that the point must remain open to new data from research work on several related fields. For instance, many more *in natura* observations are badly needed; Labouriau and his colleagues themselves appeal to everyone interested in the biology of the cerrados to undertake such observations. Also Warming has left the question open to further, more reliable information.

This paper is intended to contribute some data on the early development of a number of cerrado woody species, from seed germination, under culture conditions. No doubt, such data will bear upon the afore said point. It is hoped, before all else, that the present study regarding the growth of the primary root during the time that covers the drought period (i.e., the first 4-7 months) will help, when more data of other sorts are available, to determine whether the young plants come from seed can, or cannot, become established on a grand scale in the cerrados (wooded savannas which clothe most of the Brazilian Central Plateau over more than 1,500,00 square kilometers, and stretch as far south as Paraná and as far north as Amazonas; see Fig. 1 & 2).

Materials and Methods

The seeds were collected at different localities in the States of Minas Gerais and Goias by the author and by Dr. Ezechias P. Heringer, whose help the writer wishes to acknowledge. A number of visits to the extensive cerrado area which extends over those tracts were made for this purpose.

Two sets of cultures were carried out, one by the author in Rio de Janeiro, under a climate of rain forest, and the other at Paraopeba (Minas Gerais), under

cerrado climate, by Dr. Inael M. da Silva, to whom the present writer is indebted for a number of important data.

The Rio de Janeiro cultures were undertaken as follows. If not otherwise stated, the seeds were sown in cans filled with coarse brown sand derived from the *restinga* (this is a type of sclerophyll forest or scrub of medium size stretching over the Quaternary sandy plains lying beside the sea). This kind of sand contains some 47 mg % of nitrogen, and has shown itself to be the best substratum for cerrado woody plants, at least in youth. Although the cans were left outdoors, receiving both rain water and full sunlight, additional water was supplied whenever necessary. It was observed that some seedlings wither when the temperature at sunlight reaches 44C; *Vochysia thyrsoidea* Pohl even gets somewhat scorched, but recovers. The seedlings, too, died if permitted to dry up.

Only a few specimens were obtained in the Botanical Garden of Rio de Janeiro from beds prepared for the purpose in clayey soil derived from gneiss.

It should be mentioned that *Dimorphandra mollis* Benth. was able to stand

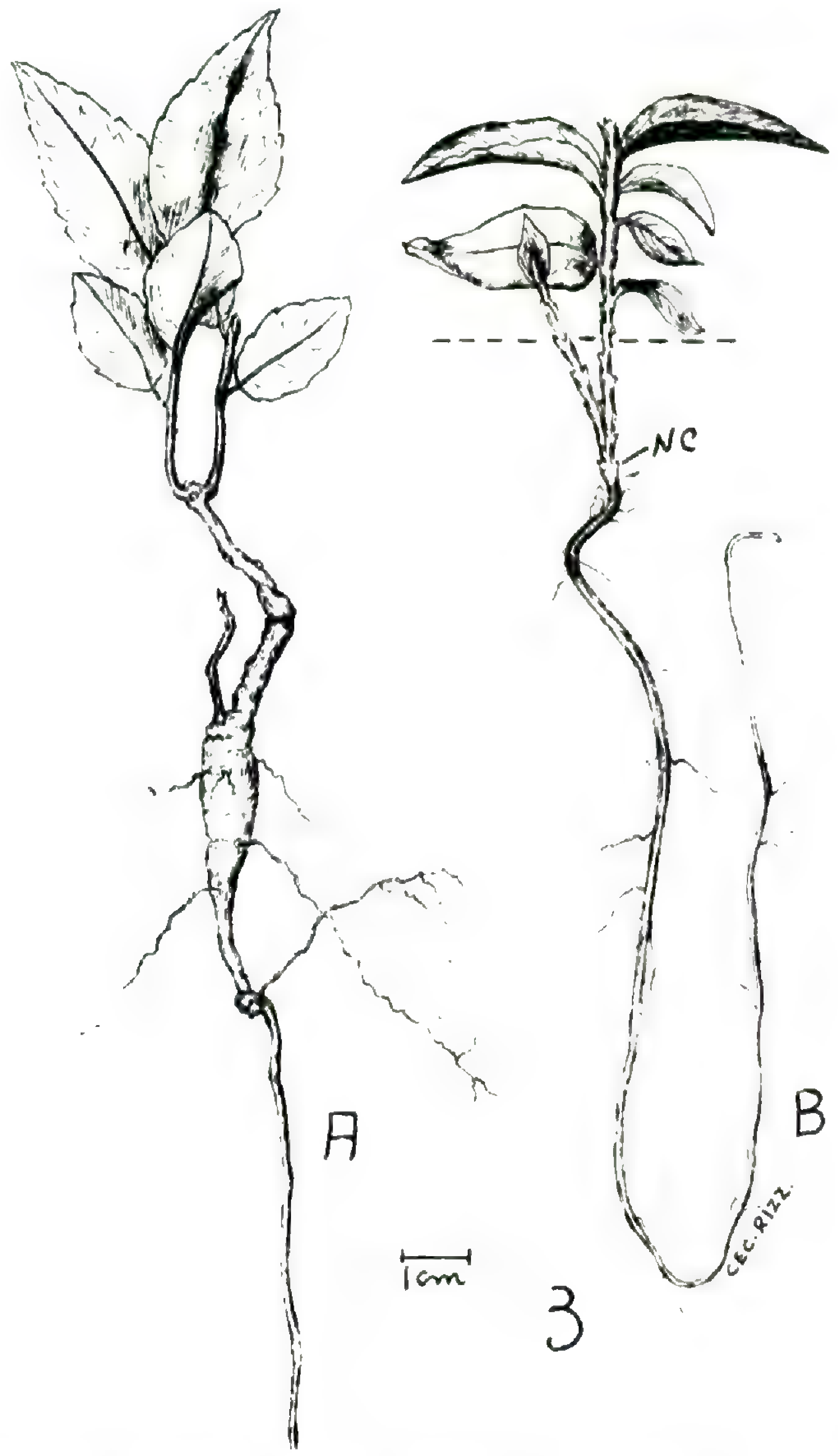

Fig. 3. A: *Plenckia populnea* Reiss., woody hypocotylar tubercle about 3 years old obtained from nature; note dead base of a previous shoot. B: *Parinarium obtusifolium* Hook. at the 7th month; note 2 shoots with underground basis.

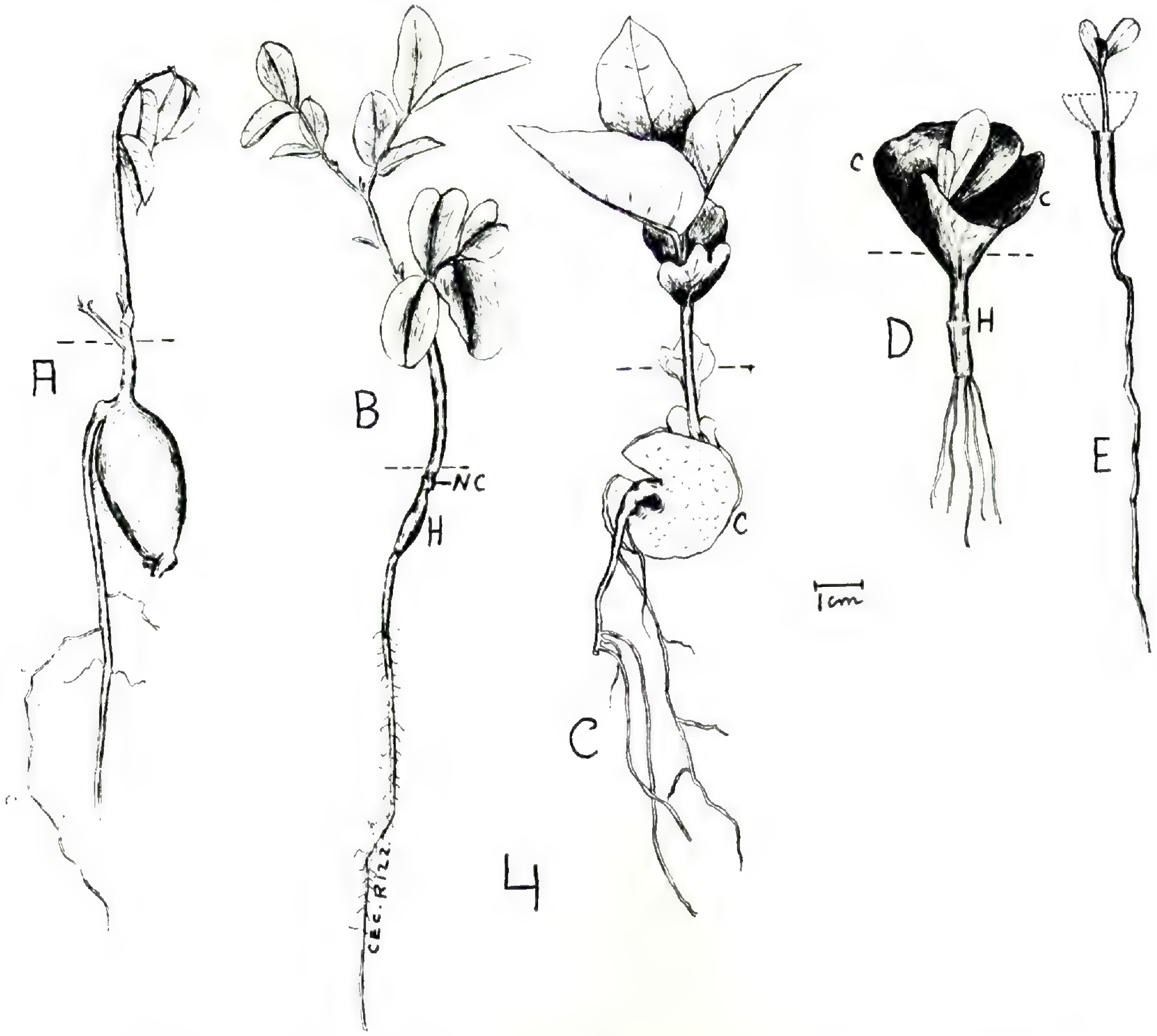

Fig. 4. Seedlings of various cerrado woody species. A: *Andira humilis* Benth., 1 month old. B: *Copaifera oblongifolia* Mart., 45 days old; note slightly thickened hypocotyl. C: *Aspidosperma verbascifolium* M.-Arg., 1 month old with large, rounded cotyledons; observe some long secondary roots arising from the remaining upper portion of the primary root which was cut off; lower leaves are lobate. D: *Vochysia thyrsoidea* Pohl, 2.5 months old showing large cotyledons in the middle of which lies the exceedingly small shoot; note several adventitious rootlets arising from the hypocotylar basis in place of the primary root which was cut off. E: *Vochysia thyrsoidea* Pohl, 2.5 months old in which the cotyledons were removed to show the poorly developed shoot; note the thick hypocotyl and the slender primary root. C, cotyledon; H, hypocotyl; NC, cotyledonary node.

shading during the early stages of growth. For about 18 months, some individuals were kept in pots in the laboratory without being touched by any sunlight. This is in accordance with the known fact that young plants of such a species live long within the overcast environment of the *cerradão*. The shaded seedlings, however, exhibited poor development in contrast with those living at full exposure.

Another remark of ecological import regards the readiness with which the seedlings can regenerate both the aerial portion and the primary root when these parts are cut off or otherwise destroyed. It is feasible, for example, to uproot the seedling by pulling and, after examination, to replace it in the soil; most of

the plants show no sign of any damage. Thus, it is an easy task to transplant the young plants without the usual care this operation requires.

At Paraopeba, Dr. Inael prepared several beds in the very cerrado soil, in which he sowed a large amount of seeds gathered from many cerrado trees. Thus, germination and the early development of his plants were conducted at full exposure; but some other plantlets proceeded from the nursery, and were transplanted with care so as not to injure their primary root.

Some other data from Paraopeba, however, come from earlier experiments by Dr. Ezechias P. Heringer, the well-known cerrado researcher. Still other data from this locality were assembled by the present writer during various sojourns there; they refer almost exclusively to plants cultivated under shelter in the nursery. Paraopeba has a well-defined dry season usually lasting some 6 months, which was compensated by irrigation of the experimental beds.

Seedling Development

As an introductory remark, one should point out that, with very few exceptions, trees and shrubs thriving in the cerrado exhibit deep taproots. At an early age, a number of species present a thickened central organ either composed from the hypocotyl or more often from the primary root (Fig. 3A); they are tuberized, short, drought-resistant, root systems. Most species, however, possess long, rather slender taproots from the beginning of development (Fig. 3B, 5). Exceptions to these rules are *Thieleodoxa lanceolata* (Hook.) Cham. and *Casearia sylvestris* Sw., both of which are originally small forest trees; their root systems, for a number of months, proved to be poorly developed, tiny, and slow-growing (Fig. 5D).

Vochysia thyrsoidea Pohl, a conspicuous representative of the cerrado woody flora, also departs from the normal pattern of development. Seeds thereof only germinate at the soil surface, emitting two cotyledons which grow large (2-3 cm in length) as well as succulent and fleshy; the hypocotyl, which appears at the same time, is thick, watery, and prolonged downwards by a slender primary root. The cotyledons are the assimilatory organs of the seedling for no leaves arise at this stage. The shoot, bearing foliage leaves, scarcely starts to grow out by the third month; the first two leaves are very minute and remain for a long time (at least one year) between the cotyledons; yet the taproot keeps on growing, reaching about 12 cm by the third month (Fig. 4, D & E).

In some species, among the most common ones in cerrado, the taproot is given off and develops for months before the stem meristem of the embryo starts its growth. In such instances there arises a long root from the seed without any shoot. Only when the root attains some 15-30 cm does the above-ground portion commence to emerge. This has been observed in *Andira laurifolia* Benth., *Pouteria torta* (Mart.) Radlk., and *Annona crassiflora* Mart. The same phenomenon was previously reported by Gentry (1952) in *Simmondsia chilensis* (Link) Schne. (jojoba), from Mexican deserts; its seeds send down a root 30-45 cm in length before the shoot arises. In these and other species the cotyledons remain unchanged for more than 2 years inside the seed-shell, in the ground.

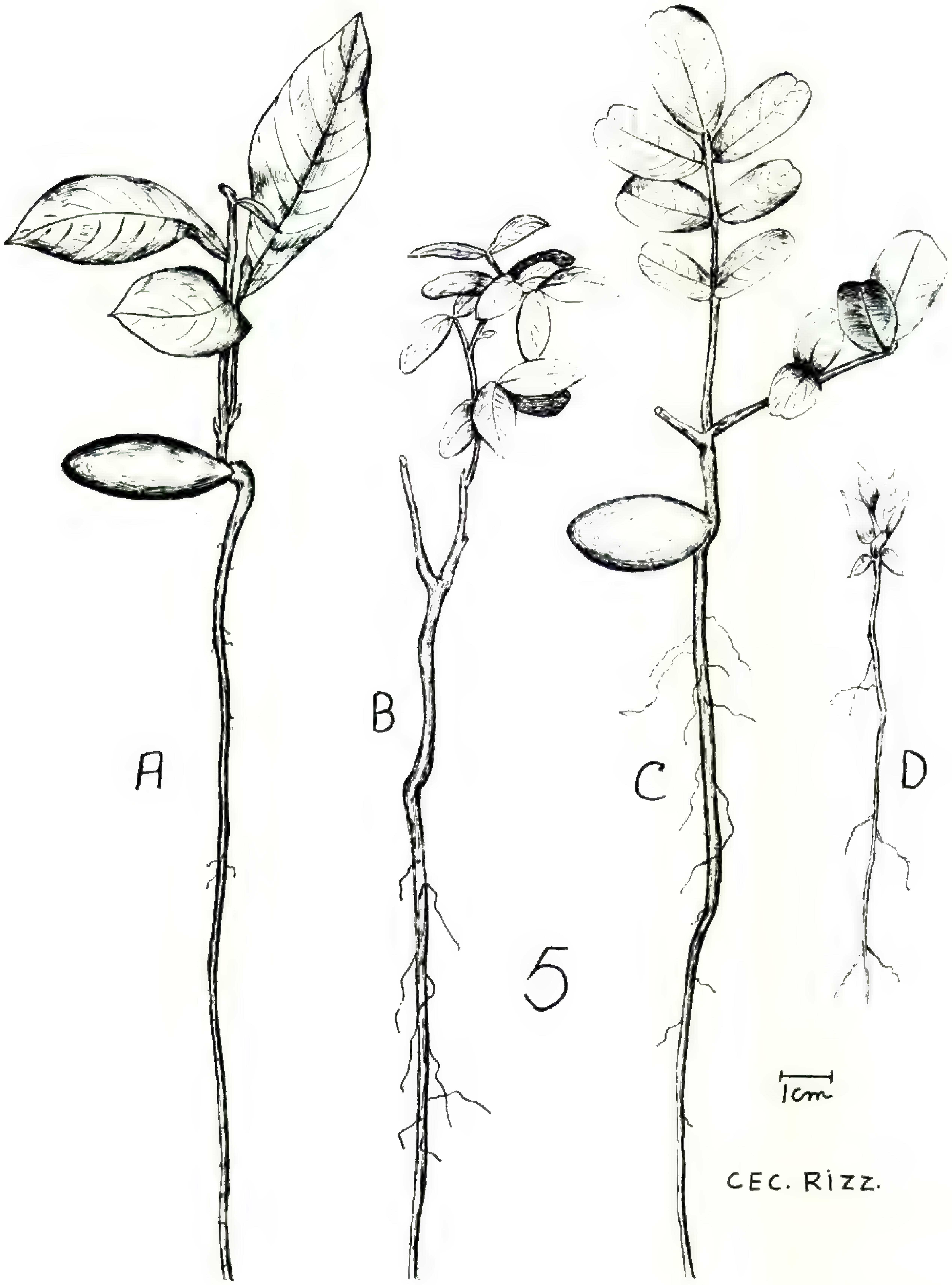

Fig. 5. Plantlets of some cerrado woody species. A: *Pouteria torta* Mart., at the 9th month. B: *Copaifera oblongifolia* Mart., at the 10th month. C: *Andira humilis* Benth., at the 7th month. D: *Thieleodoxa lanceolata* (Hook.) Cham., at the 4th month; note the short primary root.

Table 1. Data from species grown in Rio de Janeiro in *restinga* coarse brown sand.

Species	Age months	Root cm	Shoot cm	Germinat. type	Germinat. time	Germinat. %
Peschiera affinis (M.-Agr.) Miers var. *campestris* Rizz., *Apocynaceae*	2	15	7	epig.	90-127 d	75
Terminalia argentea Mart. & Zucc., *Combretaceae*	2	12	16	epig.	47 d	15
Spiranthera odoratissima St.-Hil., *Rutaceae*	2	11	4	hypog.	45-62 d	28
Hancornia speciosa Gomez, *Apocynaceae*	3	12	8	epig.	30 d	—
Mimosa clausenii Benth., *Leguminosae*	3,5	13	7	epig.	6-10 d	100
Thieleodoxa lanceolata (Hook.) Cham., *Rubiaceae*	4	8	3	epig.	65-80 d	10
Casearia sylvestris Sw. var. *lingua* Eichl. f. *campestris* Eichl., *Flacourtiaceae*	4	8	3	epig.	40-60 d	20
Cassia mystacicarpa Rizz. & Her., *Leguminosae*	5	12	9-12	epig.	11-18 d	100
Dimorphandra mollis Benth., *Leguminosae*	5	25	14	epig.	3-7 d[a]	100
Andira humilis, *A. laurifolia* Benth., *Leguminosae*	5-9	25-35	5-12	hypog.	32 d-8 m	66
Annona crassiflora Mart., *Annonaceae*	6	30	8	epig.	7–10 m	75
Esenbeckia pumila Engl., *Rutaceae*	6	15	3	hypog.	28-35 d	40
Mimosa laticifera Rizz. & Mattos, *Leguminosae*	7	20	90	epig.	6-10 d	100
Parinarium obtusifolium Hook., *Rosaceae*	7	31	3	hypog.	6 m	25
Chrysophyllum soboliferum Rizz., *Sapotaceae*	7	15	only leaves	hypog.	34-62 d	90
Erythrina mulungu Mart., *Leguminosae*	8	16	10	epig.	30 d	90
Anemopaegma arvense (Vell.) Stell., *Bignoniaceae*	8,5	22	10	hypog.	14-23 d	90
Astronium fraxinifolium Schott, *Anacardiaceae*	9	30	6	—	—	—
Enterolobium ellipticum Benth., *Leguminosae*	9	75	30	epig.	3 d[a]	80
Platypodium elegans Vog., *Leguminosae*	9	22	15	hypog.	—	15
Magonia pubescens St.-Hil., *Sapindaceae*	9	30	6-10	hypog.	20-40 d	50
Pouteria torta Mart., *Sapotaceae*	9	40	5-6	hypog.	37-90 d	100
Vochysia thyrsoidea Pohl, *Vochysiaceae*	9,5	25	3	epig.	40 d	60
Copaifera oblongifolia Mart., *Leguminosae*	10	25	6	hypog. or semi-epig.	20-35 d	58
Sclerolobium aureum Benth., *S. paniculatum* Benth., *Leguminosae*	10	15-25	10	epig.	12 d	40-60
Stryphnodendron confertum Her. & Rizz., *Leguminosae*	13	26–30	3-4	epig.	9-11 d	50

[a] Oven.

Observations—A few seeds of *Andira* and *Pouteria* required respectively 8 and 6 months to germinate. Some seeds were placed to germinate in a moist chamber at 30 C. In *Peschiera affinis* the primary root is 30 cm long by the 8th month.

Table 2. Data from species raised at Paraopeba in cerrado soil.

Species	Age, days	Root, cm	Germinat. time	Germinat. %	Root at 12 m
Astronium fraxinifolium Schott (forest)	103	26	17 d	90	50 cm
Astronium urundeuva (Fr. All.) Engl.	129	14	9 d	90	47
Dimorphandra mollis Benth.	106	12	19 d	30	—
Terminalia argentea Mart. & Zucc.	81	29	33-39 d	70	34
Piptadenia macrocarpa Benth.	88	44	4-5 d	80	—
Mimosa laticifera Rizz. & Mattos	117	16	13 d	90	98
Plathymenia foliolosa Benth. (forest)	126	20	8 d	80	65
Plathymenia reticulata Benth.	90	11	17 d	50	18
Bowdichia virgilioides H. B. K.	102	23	33 d	40	—
Dipteryx alata Vog.	23	16	12 d	90	31
Magonia pubescens St.-Hil.	35	17	11 d	70	28
Caryocar brasiliense Camb.	47	20	73 d	50	—
Piptadenia communis Benth. (forest)	78	24	7 d	90	53

Observation—Magonia pubescens, in Rio de Janeiro at age 1 month shows a taproot 10-12 cm long; other data in Table 1.

A summary of the most important results concerning the bulk of the species investigated in Rio de Janeiro is presented in Table 1. The following features were taken into account:

1. Age of the seedlings in months.
2. Length of the primary root in centimeters.
3. Height of the primary shoot in centimeters.
4. Germination type, whether epigeal or hypogeal.
5. The time germination takes, in days or in months, to send up either the cotyledons (epigeal germination) or the plumule (hypogeal germination).
6. Percentage of germination.

The data from cultivation of some cerrado species at Paracopeba are listed in Table 2, which includes also a few forest species for the sake of comparison. These data were provided by Dr. Inael M. da Silva. The features considered were the following:

1. Age of the seedlings in days.
2. Length of the primary root in centimeters.
3. Time consumed by germination in days.
4. Percentage of germination.
5. Length attained by the taproot at one year; in this case, the 12 month period was counted from the day on which the seedlings were transplanted from the nursery to the cerrado beds; the seedlings were already 2-6 months old when taken into the open.

Table 3 presents some additional data obtained years before from old cultures by Dr. Ezechias P. Heringer as well as some others drawn from Rizzini & Heringer (1962a). Although they are rather miscellaneous, they may have a bearing upon the problem of cerrado regeneration.

As may be seen from the tables, none of the plant species thriving in the cerrado, over one year (one drought period), has succeeded in sinking its taproot into the ever-wet portion of the soil, that is, below 1 m. Table 3 shows plainly that, after two years, several of them have not yet attained this depth even in cerrado surroundings. In the instance of two species, one from forest, the other from savanna—*Astronium fraxinifolium* and *A. urundeuva, Plathymenia foliolosa* and *P. reticulata*—the cerrado entities seem to be at a disadvantage as to the rate growth of the primary root, under the same conditions for both species.

Figure 5 illustrates four such species grown in Rio de Janeiro at early stages of development. It is to be noticed that the primary root is far longer than the first shoot, which is remarkable for its slow rate of growth. Seedlings are shown in Fig. 4.

Leaf Change

The majority of the seedlings held in culture in the moist climate of Rio de Janeiro, and receiving additional water whenever the weather is sunny, do not shed their leaves during the months which comprise the cerrado dry season, namely, from May to September. Instead they produce new leaves mostly in October, though they may sometimes do so as early as September; by November they exhibit

Table 3. Miscellaneous data from species cultivated at Paraopeba in cerrado soil, combined with other data drawn from Rizzini & Heringer (1962a).

Species	Age, months	Root, cm	Shoot, cm
Anemopaegma arvense (Vell.) Stell.	6	30	9
Caryocar brasiliense Camb.	10	80	40
Dalbergia violacea (Vog). Malme	12	32-37	10-22
Hymenaea stigonocarpa Mart.	12	45	34
Kielmeyera coriacea (Spr.) Mart.	12	23–35	7–8
Erythrina mulungu Mart.	24	15	8
Sclerolobium aureum Benth.	24	85	13
Anacardium pumilum St.-Hil.	27	80	15
Hancornia speciosa Gomez	24	60	40
Kielmeyera corymbosa (Spr.) Mart.	24	40	12
Ouratea sp.	24	30–40	2–5
Stryphnodendron barbatimao Mart.	24	40	20
Sweetia lentiscifolia (Schott) Spr.	24	40	14
Plenckia populnea Reiss.	24	4–9	2–5

Observation—A. arvense and *A. pumpilum* are undershrubs, though the latter grows into a tree in the genial climate of Rio de Janeiro reproducing by seed from typical undershrub plants.

their fresh small leaves. Thus, the replacement of the old leaves by the new ones proceeds gradually, the former standing rather long together with the latter. The following account describes the behavior shown by some species.

Mimosa multipinna Benth., *Peschiera affinis* (M.-Arg.) Miers var. *campestris* Rizz., *Pouteria torta* Mart., *Chrysophyllum soboliferum* Rizz., *Sclerolobium paniculatum* Benth., *Andira laurifolia* Benth., *A. humilis* Benth., *Copaifera oblongifolia* Mart., *Thieleodoxa lanceolata* (Hook.) Cham., *Vochysia thyrsoidea* Pohl, and *Dimorphandra mollis* Benth., have been observed to emit new leaves from October to November, the earlier ones still remaining and being shed little by little; these leaves can even last for a number of months after they are one year old.

Decidedly deciduous species are far less numerous; they loose their leaves under any climate, as *Esenbeckia pumila* Engl., *Stryphnodendron confertum* Her. & Rizz., *Erythrina mulungu Mart.*, and *Bombax* sp. They become leafless about June. The leaves gradually turn yellow before falling off and the falling itself is also gradual. *Annona crassiflora* Mart. deserves special mention for it sheds its leaves almost altogether; however, the new ones begin to burst as early as September when there are still one or other of the old leaves left.

Fresh shoots are also laid down at the same time, almost always from the cotyledonary node which lies at the stem basis; in most plants this part is hidden beneath the ground surface. Adventitious reparative buds can, too, be easily formed there.

In the Botanical Garden of Rio de Janeiro there is a small cerrado stand some 30 years old. The savanna trees do very well in the humid climate and clayey soil which prevail there, as Fig. 6 and 7 illustrate. Due to such a climate, the grass cover, composed of grasses not peculiar to the cerrado, attains great development, keeping green the year round.

Fig. 6-7. Cerrado stands at the Botanical Garden of Rio de Janeiro. Fig. 6 (left) illustrating in the foreground *Tabebuia ochracea* Cham. displaying corky bark; notice the grass cover. Fig. 7 (right) illustrating *Thieleodoxa lanceolata* (Hook.) Cham. in fruit.

In such a man-made cerrado it is noted that new leaves are set out between October and November. *Copaifera langsdorffii* Desf., *Sweetia dasycarpa* (Vog.) Benth., *Hymenaea stigonocarpa* Mart., *Caryocar brasiliense* Camb., *Lafoensia sp.*, *Tabebuia ochracea* Cham., *T. alba* Cham., *T. caraiba* (Mart.) Bur., *Fagara sp.*, *Anacardium humile* St.-Hil., *Plathymenia reticulata* Benth., *Thieleodoxa lanceolata* (Hook.) Cham., *Diospyros sericea* DC., and so on, were seen to behave as has just been referred to above. For an account of the cerrado flora the reader must see Warming's (1892) classical work and Rizzini's (1963) modern one.

These facts, together with others mentioned before (see Introduction), seem to suggest that the woody plants peculiar to the cerrados appreciate increased humidity.

Naturally occurring cerrados never become entirely leafless, although the shedding of leaves is intense. The leaves fall off gradually in the course of the drought period, but not altogether, and the new leaves start to spring as soon as the rains come or even before their coming. This means that, as is generally admitted, the soil water reserves are just sufficient to maintain the savanna in a state of reduced life activity; accordingly, a number of species either blossom or set fruit during the dry season. It is interesting to notice that the development of fresh leaves occurs simultaneously both in Rio de Janeiro and in the cerrado, i.e., mostly in October at the two areas.

The worst hindrance to vital processes in the cerrado is the fire annually set

by cattlemen and by farmers, which sweeps the savannas on a gigantic scale the wide world over. Fire cannot fail to have a profoundly harmful influence on such a vegetation like the cerrado which is richly supplied with dried, easily burning remains during several months. The reader is referred to Warming (ib.) for details on this point; he notes, for instance, that fire burns the leaves and hastens the leaf-fall.

Cerrado and cerrado plants in Rio de Janeiro may be said to be far greener than they are in their natural surroundings.

Water Stored in the Underground Parts

It was decided to measure the amount of water the plants possessing thick, tuberized, subterranean organs are able to reserve in their tissues. This was accomplished in a number of cases. Pieces of these organs were placed in fully corked vials and brought to the laboratory. After their weight was estimated, the pieces were dessicated at 100C and weighed again. The amount of water is presented as percentage of the fresh weight. The plant tissues used were taken from nature unless otherwise stated. Some species from other kinds of vegetations besides the cerrado were included for comparison.

Corytholoma discolor (Lindl.) Frits., fleshy aerial tubercle from rain forest, gathered in April	90%
Cochlospermum sp. from Pernambuco, fleshy root from culture in Rio de Janeiro	85%
Cissus simsiana R. & S., root tubercle from cultivated plants	82%
Mandevilla illustris (Vell.) Woods., tuberous root	72%
Marsdenia virgultorum (Fourn.) Rothe, from limestone, fleshy root collected in July	65%
Annona crassiflora Mart., hypocotylar tubercle with fleshy cortex, 3 months old, from culture	60%
Plenckia populnea Reiss, hypocotylar ligneous tubercle with thick, soft cortex	59%
Chrysophyllum soboliferum Rizz., underground shoot (subole) with thick, soft cortex	57%
Manihot gracilis M.-Arg., fleshy, starchy root	57%
Terminalia argentea Mart. & Zucc., woody root tubercle from nursery	56%
Piptadenia macrocarpa Benth., the same as above	48%
Piptadenia falcata Benth., woody root tubercle	44%

There follow four additional results from Rachid (1947).

Craniolaria integrifolia Cham., big fleshy root	up to 91%
Ipomoea villosa Meissn., tubercle	80%
Manihot tripartita M.-Arg., root tubercle	87%
Cochlospermum regium (Mart. & Schr.) Pilg., fleshy root	75%

Had the dry weight been taken into consideration, the water percentage, for example in the tubercles of *Corytholoma discolor*, would amount to 876% instead of 90%.

Comments

The data so far obtained seem to indicate that no taproot goes down below 1 m at an age of 1-2 years or, putting it differently, young plants must survive at least 1-2 drought periods with their main root placed in the driest part of the soil (the rainless season in the cerrado commonly lasts 6 months, and is characterized by a very clear sky). At first glance *Caryocar brasiliense* would be a possible

exception, according to the data in Table 3; however, the plants from which the measures were taken were copiously irrigated ones (see Rizzini & Heringer, 1962a).

That roots of many plant species can survive soil dryness well beyond the wilting point is obvious from observations in arid and semi-arid countries and, according to some authors, roots can even grow in dry soil. Even conifers may be cited in this connection. Stone (1958) mentions that seedlings of *Pinus ponderosa, Libocedrus decurrens,* and *Abies concolor* can stand, respectively, 64, 44, and 35 days in a soil devoid of any available water. Moreover, he points out that application of artificial dew during night to such plantlets suffices to keep them alive for 30, 72, and 20 days more, while the soil remains in the same waterless condition. Thus, the three species can bear a period of water shortage in the soil embracing about 2-3-4 months, at least under experimental conditions. Conifers are interesting in this concern because they carry a number of "xerophytic" devices though they do not live in dry habitats in the usual sense.

The present writer found that in a well-developed dry forest at Sete Lagoas (Minas Gerais) a rather abundant regeneration of plants of *Hymenaea stilbocarpa* Mart. preserved their leaves in a good condition in the middle of the dry season. One of these young plants, about 1 year old, bore a primary root some 30 cm long, yet the soil around it carried only 7% water, certainly below the wilting point.

Keeping in mind such considerations, it is desirable to direct attention to the means through which relatively slender roots will be able to go through a rainless period sunk in a dry substratum.

The ability of roots to endure soil dryness in countries possessing a drought period may well be connected to the precocious as well as far more intense *lignification and suberization* that are known to take place in both roots and shoots of plants thriving under dry, sunny conditions (Warming, 1909, who gives a full account of this subject, which is sharply commented and enlarged on by Milanez, 1951; Killian & Lemée, 1956). These cell wall modifications represent efficient devices against drought and heat effects. A further, no less important fact to recall is the *deposition of pectin* in the walls of the root cap cells. As is known, pectin is a highly water-holding substance which is apt to keep the root growing point in a good state of turgescence preventing it from dessecating, despite the dryness of the medium. It is to be pointed out that heavy lignification and suberization are quite well-known in the savannas, macchia, cerrado, campo, and other areas.

The above considerations seem definitely to displace the problem of the establishment in dry habitats to the *very early stages of seedling development*—when the cell wall contrivances have not yet attained full development and consequently the young plants are not able to withstand drought. It follows that the *real critical period would be the first drought season* to be passed through by the seedlings, subsequent to seed germination. Thus the data afforded by this paper on the length of the primary root of cerrado plants, in the course of such period, may help in solving the issue when other data are available.

The critical point is to ascertain (a) whether the seeds can in fact germinate, and (b) whether the minute seedlings can bear the harsh conditions of soil and

drought that prevail in the environment of most cerrados. Ferri (1961a), as mentioned earlier in this paper, claims plainly that both cannot: "And when some germination occurred the final survival of seedlings was extremely low." Under milder conditions, such as those reported in this paper, they developed quite well. Rizzini & Heringer (1962a) think that the swift growth the taproot possessed at early stages in many such seedlings would "enable the plants to withstand the drought period with the absorbing part of the roots sink into the ever-wet portion of the ground *wherever the spot be favorable.*" But the same authors (ib.) remark that such a spot "rarely occurs in the *far touched cerrados,* which is exactly the type found in the most parte of their range."

It may be said that the rate growth of the primary root, whether in Rio de Janeiro or at Paraopeba, is about equal. In the few cases in which a comparison was possible in the same species (*Magonia, Terminalia, Anemopaegma*), the cerrado-grown ones showed a slightly better rate of growth.

One cannot leave out a consideration of the role that fire, so wide-spread in the cerrados, most probably plays in the destruction of seedlings. Seeds, too, are liable to perish by fire (Warming, 1892; Rizzini, 1964). Ferri (1961a) as well as Rizzini (ib.) draw attention to the high degree at which seeds are destroyed in cerrado by insect larvae.

Of no less importance is to take into due consideration the *high powers of regeneration* the seedlings proved to have, after serious traumas, when well watered. Under the heading of MATERIALS AND METHODS this peculiar property has already been referred to. Attention should be drawn to the fact that the regeneration ability shown by seedlings is in accordance with the sprouting ability of the corresponding adult plants, which set forth coppice shoots freely from both aerial stumps and even underground portions, not to mention their normal yearly sprouting from the branches. The role played by this outstanding feature in the seedling stage has not yet been ascertained in regard to the establishment of the plants in their habitat.

Germination features also deserve some comment. Table 1 shows that the epigeal type of germination predominates largely over the hypogeal one. In broad terms, the epigeal type belongs to trees (exceptions are only *S. confertum* and *P. affinis*, undershrubs), while the hypogeal type is typical of six morphologically very similar undershrubby species, though they are quite unrelated from a taxonomic viewpoint (exceptions are only the trees *P. elegans, M. pubescens, and P. torta*). *C. oblongifolia* is transitional between the two groups; although most of its seedlings exhibit underground cotyledons, some send them up into the air. The voluminous seeds of *Caryocar brasiliense* (not included in Table 1) germinate hypogeally.

Among the plants of the hypogeal group excel large-seeded species. Nevertheless, *S. odoratissima, E. pumila,* and *P. elegans* belong here and they have decidedly small seeds.

The seeds of *Annona crassiflora* rank first in regard to the amount of time they require to germinate for, although not especially hard-shelled, they consume as much as 7-10 months. Next to them rank the seeds of the *Andirae.* However,

in these species the seeds are not enclosed in a shell as hard as that of *Parinarium obtusifolium*, whose seeds take about 6 months to germinate.

Finally, species provided with water-storing underground structures at early stages, though obviously present, do not make up the bulk of the flora. The major part thereof displays long, slender taproots.

This is not the right place to draw definitive ecological implications from the data assembled here for they evidently need to be tied to data of other sorts.

Acknowledgments

The author wishes to express his deep appreciation for the help received from the Conselho Nacional de Pesquisas which has contributed both continual encouragement and financial support, and from Dr. Bertha Lutz (Museu Nacional) for reading the manuscript. The assistance of Dr. Inael Maximo da Silva and of Dr. Ezechias Paulo Heringer in obtaining seed and plants from different cerrados, and helpful information concerning the matters dealt with in the present paper, is gratefully acknowledged.

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ON THE STATE OF THE CONGO FLORA

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As a tribute to my good friend, the late Dr. R. E. Woodson, Jr., the initiator of an illustrated Flora of Panama, a short note on the origin and progress of the Congo Flora may here not be out of place.

I. After my first botanical exploration of the former "Congo Belge et Ruanda-Urundi," in 1925-1926, I put forward, in June 1927, the idea of publishing a regional flora of that great geographical area of central Africa, fitting in with the plan of regional intertropical African floras elaborated at the Royal Botanic Gardens, Kew.

At that time, the Congo flora was rather incompletely known, notwithstanding the numerous publications of the late Dr. É. De Wildeman. Important and rapidly growing herbarium material deposited at the State Botanical Garden, Brussels, was waiting to be worked out. Moreover, due to the political boundaries, the area covered most of the diverse vegetation and floristic territories of intertropical Africa, making the task of writing a flora rather difficult.

After the foundation of the "Institut National pour l'Étude Agronomique du Congo Belge" or I.N.É.A.C. in December 1933, it became soon obvious that a scientific and up-to-date knowledge of the flora was basic for a rational exploitation of the renewable resources of the country and especially for its agricultural expansion.

In 1942, during the second world war, a provisional joint Committee was set up by the I.N.É.A.C. and the State Botanical Garden to consider appropriate means for publishing the Flora in question.

A scheme was outlined for the publication of a general Flora, subdivided into several parts: a Flora of the Spermatophytes, a Flora of the Pteridophytes, a Flora of the Bryophytes and a Flora of the Thallophytes.

The main directions for the preparation of the general Flora were fixed as follows:

1. The study, made by families, is to be based on a critical revision of all herbarium material of the area available at Brussels and in other herbaria.
2. Workable analytical keys for all taxa of infra-family rank must allow the determination not only of the herbarium material, but also of living plants in the field.
3. For each taxon a full description is to be given according to a standard sequence.
4. The bibliography and synonymy must be given fully, but restricted to the area concerned.

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5. The geographical distribution must be indicated inside the phytogeographical territories of the area (see map, Fig. 1), by citation of controlled and representative specimens. The type specimen is to be cited when it is collected inside the area.
6. The general distribution outside the area is to be given as accurately as possible.
7. Indications on the habitat, as well as native names and uses, must be added.
8. If necessary or useful, taxonomic remarks and other notes will be given at the end.
9. All exotic taxa are to be printed in smaller type and without numbering.
10. All new taxa are to be published with descriptions in the Bulletin of the State Botanical Garden, but all new combinations and synonyms must be given in the Flora.
11. Original line drawings, mainly plates with habit and analyses of reproductive organs on a standard scale, at least one per genus or one per group of 10 species, will be supplied with indication of the specimen or specimens on which they are based. Other illustrations may be added.

Considering their prime importance and the rich available herbarium material, it was decided to start the general Flora with that of the Spermatophytes.

An Executive Committee of the Congo Flora, presided over by the Director of the State Botanical Garden, was entrusted with the scientific direction of that Flora, the families of which should be published in the systematical sequence of the Engler system.

General instructions were provided for the collaborators, who had to work at the State Botanical Garden, where the extensive library, the herbarium collections and all working facilities were put at their entire disposal. On the other hand, financial support was given by the I.N.É.A.C., not only for the salaries of the permanent collaborators, apart from the members of the Garden staff, but also for the cost of publication. Occasional collaborators were invited on contract.

The Flora is prepared by the Executive Committee and the State Botanical Garden and published, in 8° size, at Brussels by the I.N.É.A.C. It bears the title "Flore du Congo Belge et du Ruanda-Urundi—Spermatophytes" for the volumes I to VII and IX and for the analytical key of the families. Volumes VIII(1) and X appeared after the Congo Independence under the altered title "Flore du Congo, du Rwanda et du Burundi—Spermatophytes."

Shortly after the Congo Independence, the I.N.É.A.C. was dissolved, and the Executive Committee had no more power to act. The whole organisation was then taken over by the Belgian Government and volume XI, currently in preparation, will probably be issued in the course of 1965 under the auspices of the State Botanical Garden. The future and the continuation of the Flora are hereby assured.

The list, with the contents, of the actually published volumes of the "Flore des Spermatophytes" is as follows:

1948—Volume I: *Cycadaceae, Podocarpaceae, Cupressaceae, Gnetaceae, Piperaceae, Hydrostachyaceae, Myricaceae, Ulmaceae, Moraceae, Urticaceae, Podostemaceae, Proteaceae, Olacaceae, Opiliaceae, Octoknemaceae, Santalaceae, Loranthaceae, Aristolochiaceae,*

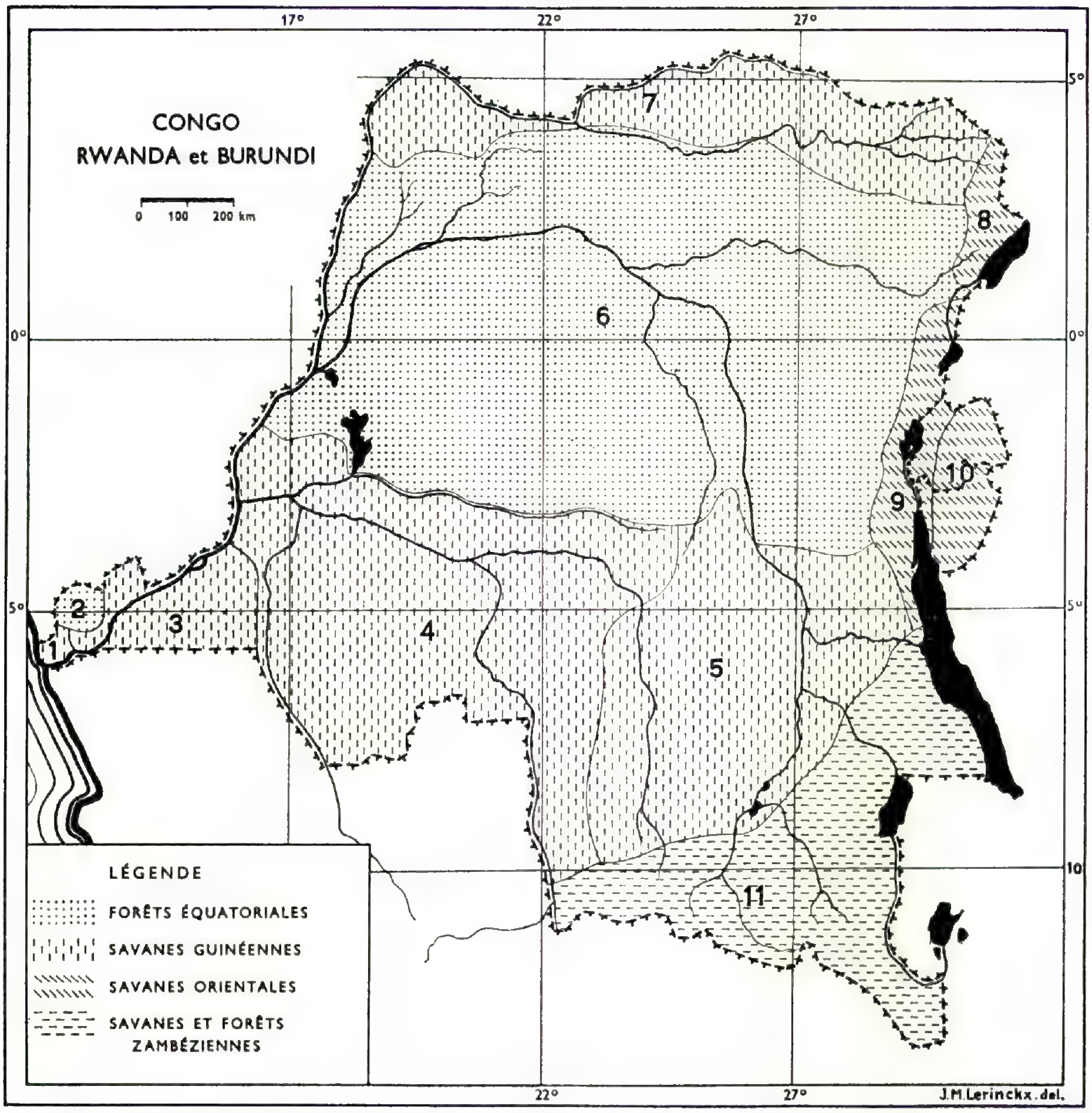

Fig. 1. Phytogeographical Territories after W. Robyns. -1. Coast. -2. Mayumbe. -3. Lower-Congo. -4. Kasaï. -5. Lower-Katanga. -6. Central Forest. -7. Ubangi-Uele. -8. Lake Albert. -9. Lakes Edward and Kivu. -10. Rwanda-Burundi. -11. Upper-Katanga.

Rafflesiaceae, Hydnoraceae, Balanophoraceae, Polygonaceae; 446 p., XLI pl., 1 col. front., 1 col. pl., 3 fig., 12 phot.

1951—Volume II: *Chenopodiaceae, Amaranthaceae, Nyctaginaceae, Phytolaccaceae, Aizoaceae, Portulacaceae, Basellaceae, Caryophyllaceae, Nymphaeaceae, Ceratophyllaceae, Ranunculaceae, Menispermaceae, Annonaceae, Myristicaceae, Monimiaceae, Lauraceae, Hernandiaceae, Fumariaceae, Capparidaceae, Cruciferae, Resedaceae, Droseraceae, Crassulaceae, Pittosporaceae, Hamamelidaceae;* 609 p., LVII pl., 1 col. front., 9 fig., 5 phot.

1952—Volume III: *Rosaceae, Connaraceae, Mimosaceae, Caesalpiniaceae;* 579 p., XL pl., 1 col. front., 46 fig., 15 phot., 1 map.

1953—Volume IV: *Papilionaceae,* part 1; 314 p., XVIII pl., 20 fig., 1 map.

1954—Volume V: *Papilionaceae,* part 2; 377 p., XXVII pl., 25 fig., 1 phot., 1 map.

1954—Volume VI: *Papilionaceae,* part 3; 426 p., XXXII pl., 18 fig., 1 map.

1958—Volume VII: *Pandaceae, Oxalidaceae, Geraniaceae, Linaceae, Erythroxylaceae, Lepidobotryaceae, Zygophyllaceae, Balanitaceae, Rutaceae, Irvingiaceae, Simaroubaceae, Burseraceae, Meliaceae, Malpighiaceae, Vochysiaceae, Polygalaceae, Dichapetalaceae, Callitrichaceae;* 367 p., XXXVI pl., 11 fig., 1 phot., 1 map.

1958—Tableau analytique des familles; 69 p.

1962—Volume VIII(1): *Euphorbiaceae,* partim; 214 p., XIII pl., 16 fig., 4 phot., 1 map.

1960—Volume IX: *Buxaceae, Anacardiaceae, Aquifoliaceae, Celastraceae, Hippocrateaceae, Salvadoraceae, Icacinaceae, Sapindaceae, Melianthaceae, Balsaminaceae, Rhamnaceae, Vitaceae, Leeaceae;* 597 p., LVI pl., 14 fig., 3 phot., 1 map.

1963—Volume X: *Tiliaceae, Malvaceae, Bombacaceae, Sterculiaceae, Huaceae, Scytopetalaceae;* 352 p., XXX pl., 6 fig., 1 map.

A general account of all the indigenous taxa treated in these volumes is given in the following table, to which has been added, for comparison, the corresponding account for 1940[1]:

Dates	Families	Genera	Species	Infraspecific taxa
1963	90	599	3,171	480
1940	80	563	3,305	425
Differences	+10	+36	-134	+55

Commenting briefly upon this table it appears:

1. The increase in the number of families is partly due to the discovery of families unknown in 1940: *Cupressaceae, Hydnoraceae* and *Hamamelidaceae* and partly to the splitting of some families as the *Leguminosae* into: *Mimosaceae, Caesalpiniaceae* and *Papilionaceae,* and the treatment of *Lepidobotryaceae, Balanitaceae, Irvingiaceae, Leeaceae* and *Huaceae* as separate families.
2. The total number of genera has increased by 36 among which 24 are new: *Beirnaertia* Louis ex Troupin; *Hyalosepalum* Troupin; *Leptoterantha* Louis ex Troupin; *Exellea* Boutique; *Toussaintia* Boutique; *Afroguettaria* Boutique; *Atopostema* Boutique; *Gilbertiella* Boutique (Volume II).—*Lebruniodendron* J. Léonard; *Gilbertiodendron* J. Léonard; *Michelsonia* Hauman; *Pseudoberlinia* Duvign.; *Pseudomacrolobium* Hauman (Volume III). — *Robynsiophyton* Wilczek (Volume IV.)—*Humularia* Duvign. (Volume V).—*Pseudoeriosema* Hauman; *Haydonia* Wilczek; *Clitoriopsis* Wilczek (Volume VI).—*Flabellariopsis* Wilczek (Volume VII).—*Cavacoa* J. Léonard; *Cytharanthus* J. Léonard; *Duvigneaudia* J. Léonard [Volume VIII (1)].—*Apodostigma* Wilczek; *Bequaertia* Wilczek (Volume IX).
3. The total number of species has decreased by 134, notwithstanding the description of 533 new species which it is impossible to enumerate here.
   It is to be emphasized that the main scope of the Flora, resulting in an up-to-date knowledge, is a critical study on the species level. Many species previously cited up to 1940 were incorrectly named and had been reduced to synonyms or cited as misidentifications. Furthermore, new delimitations of taxa following a better knowledge of the available material are responsible for numerous new combinations, whereas many species are cited for the first time in the area of the Flora.
4. The infraspecific taxa, subspecies, varieties and forms, are in small progress and include 240 new taxa. Here again, the foregoing comments for the species are entirely applicable.

[1] W. Robyns, Statistiques de nos connaissances sur les Spermatophytes du Congo Belge et du Ruanda-Urundi. Bull. Jard. Bot. État Brux., **XVIII,** p. 133-144 (1946).

In conclusion, a certain compensation appears between the reduction into synonymy of the specific and infraspecific taxa on one side, and the discovery of new specific and infraspecific taxa on the other side, so that in the end the total number of these taxa known in 1940 remains nearly unaltered. Notwithstanding this situation, the balance of the work is fairly positive and represents an actual and considerable progress of our knowledge of the Congo Flora both in the field of taxonomy and of chorology. The enterprise is therefore worthy of the 28 scientific collaborators, who spared no time or efforts to produce a valuable and lasting contribution to the Flora of continental intertropical Africa.

II. In 1935 and 1936 the first two fascicles of the "Flore Iconographique des Champignons du Congo" were published at the initiative of the late M. Beeli. The Flora is based on a collection of herbarium specimens with water-color drawings of higher Fungi made in Congo by Mme. Goossens Fontana from 1919 and preserved at the State Botanical Garden. This outstanding collection has grown since to more than 1000 aquarelles, mostly with additional microscopic analyses and explanatory notes.

Unfortunately, the publication had to be discontinued after 1936 for lack of funds, but thanks to the understanding of the Ministry of Agriculture of Belgium, the State Botanical Garden was able, in 1954, to resume it, with the collaboration of several mycologists of international reputation, at the rate of one fascile per year. Each fascicle, in 4° size, comprises 3 to 4 colored plates with a corresponding text.

Actually 14 fascicles are issued as follows:

1935—Fascicle 1: Genera *Amanita* and *Volvaria.*
1936—Fascicle 2: Genera *Lepiota* and *Annularia.*
1954—Fascicle 3: *Boletineae.*
1955—Fascicle 4: Genus *Lactarius.*
1956—Fascicle 5: Genus *Agaricus* I.
1957—Fascicle 6: Genera *Agaricus* II, *Pilosace* and *Rhodophyllus.*
1958—Fascicle 7: Genus *Termitomyces.*
1959—Fascicle 8: *Cantharellineae.*
1960—Fascicle 9: *Discomycetes.*
1961—Fascicle 10: Genus *Stereum* s. l.
1962—Fascicle 11: *Xylarioideae* and *Thamnomycetoideae.*
1963—Fascicle 12: *Gasteromycetales* I.
1964—Fascicle 13: *Gasteromycetales* II.
1965—Fascicle 14: Genus *Marasmius.*

The "Flore Iconographique des Champignons du Congo" constitutes not only an important contribution to the Congo mycology, but it is also a fundamental preliminary step towards the publication of a future Flora of the Fungi, included in the scheme of the general Congo Flora.

THE IDENTITY OF SENECIO CAPILLARIS GAUDICHAUD

HAWAIIAN PLANT STUDIES 26

By Harold St. John
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Tetramolopium **capillare** (Gaud.) St. John, comb. nov.
Senecio capillaris Gaud., Bot. Voy. Uranie 468. 1830.
T. Bennettii Sherff, Bot. Gaz. **95:** 498. 1934; B. P. Bishop Mus., Bull. **135:** 11-12, *fig.* 2. 1935.

The holotype of *Senecio capillaris* Gaud. is in the Museum National d'Histoire Naturelle, in Paris. The writer examined it in 1936, and again in 1954. The species is little known, and it seems that no one has confirmed its identity since the time of Gaudichaud in 1819. The original description, with nine descriptive words, in the account by Gaudichaud, has been insufficient for a full knowledge of the plant. He described the shrubby habit, the sparse linear-capillary glabrous leaves, the leafy 1-flowered terminal peduncles. Hillebrand in his Flora of the Hawaiian Islands, 229. 1888, translated this latter, "pedunculis unifloris," as peduncles single-headed, and this was apparently true to Gaudichaud's meaning, and the 60 or so scars on the receptacle of the heads of the holotype confirm this view. Gaudichaud described the leaves as glabrous; and the older ones are so, but the young leaves are minutely glandular atomiferous when seen under a binocular dissecting microscope, such instruments not existing in 1830. In every other detail the original description exactly matches the holotype. Gaudichaud did not illustrate it, though he did so with most of his other new species.

The holotype is a single branch 29 cm long. Its naked glabrous lower stem is 10.5 cm long, reddish-brown, and at its apex parts into four strong, and one weak, upper branches which are scabrous-puberulous. The numerous leaf blades when dried are 1-2.5 cm long, 0.1-0.4 mm wide, sessile, filiform, acute, and ascending. The peduncles are 2-4 cm long, nearly naked, minutely puberulous, 1-headed. The ten heads are all post-mature, have the involucral bracts in about three rows, those of the two inner rows being subequal, 2.5-3 mm long, 0.2-0.3 mm wide, linear, tapering, acute, ciliolate, and with the center line thickened and dark. The receptacle is flat on top, with the edges rounded.

The holotype has no flowers left. None were mentioned by Gaudichaud in his description, and perhaps this lack explains why his new species was not illustrated. It well imitates the aspect of a *Senecio*, so his placement was a good guess. Now that the Hawaiian flora is better known, it is evident that *Senecio capillaris* Gaud. (1830) is the same as *Tetramolopium Bennettii* Sherff (1934) from Lahainaluna and Wainee, both on western Maui. Gaudichaud also collected in the mountains back of Lahaina, western Maui. As every detail of structure and the locality seem to coincide, the writer decided to make the necessary new combina-

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tion under *Tetramolopium*. Several days later during the 1954 visit to the museum in Paris, the writer located a 295-page folio collector's number list made by Gaudichaud on the voyage of the Uranie. For each stop he wrote a chapter, entering the plants found, and he usually added at that time a detailed description of the minute or dissected parts of the flower for each one. Notes for these details must have been made daily, but in some parts of the list it is evident that the plants or the notes had been sorted into groups, such as by placing all the ferns together. Pages 196-230 cover "Plants examinées aux iles Sandwich." In the margins of the pages are his later determinations or comments added while studying the plants in Paris. For this one his annotation is "*Senecio capillaris*." His notebook entry is "64. Syngénèse nommé Pamocani = Pamokani. Fleurs radiées-ecailles filiformes, sur plusieurs ranques, velues. Demi-fleurons de la circonference blancs, en languette, très étroites, obtuses au sommet. (ou légèremt ± Bifides?). Deux stigmates jaune-pales.

"Fleurons du centre-jaune, a cinq divisions—deux stigmates ne depassant pas la corolle. Receptacle presque plan, légerèment alvéolé, conique au centre (très légerèment conique). Fleurons et demi-fleurons chargés d'aigrettes capillaires, denticulées. Tige ligneuse. Feuilles filiformes."

This field description gives much detail for the flowers which are now missing from the specimen. The white ray flowers contrast with those of *Senecio*, and agree with the characters of *Tetramolopium*.

CONTRIBUTIONS TO THE FLORA OF TROPICAL AMERICA; LXXV[1] A NEW DACRYODES IN TRINIDAD.

By N. Y. Sandwith[2]
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In botanical literature the genus *Dacryodes* has for long been represented in the West Indies by a single species, *D. excelsa* Vahl, which is widely distributed from Puerto Rico to Grenada and is known as "Gommier" or "Bois d'encens" in the Lesser Antilles. For many years, however, I have been aware of the existence in the high forests of the Northern Range of Trinidad of a *Dacryodes* which does not agree with *D. excelsa* because of its more numerous pairs of relatively long and narrow leaflets which are firmly papery or only rather thinly leathery and conspicuously acuminate at the apex. The evidence for this distinct tree was fruiting material collected in the Arima Valley by the late Mr. W. E. Broadway in January, 1925, near the 10½ mile-post on the Blanchisseuse Road, and distributed under the name "*Astronium obliquum* Griseb.?" The tree was noted as of fairly large size, fruiting abundantly, and known as "Incense Tree," but in Trinidad, as elsewhere in the Antilles, the names "Incense" and "Gommier" are often applied to species of the genera *Protium* and *Bursera* in the same family, *Burseraceae.*

Realising the interest of this tree as belonging to a genus and species new to the Trinidad flora, I asked local botanists to look out for further examples in the forests along the Blanchisseuse Road, and to collect flowering material when possible. Nothing further was discovered about the tree until quite recently when the drupes of this very species attracted the notice of the ornithologist, Dr. D. W. Snow, who was collecting and seeking to identify the various fruits and seeds connected with feeding habits of the Oilbird, *Steatornis caripensis* Humboldt, in these forests. When he visited Kew in 1959 to ask about these drupes, which came from a species which he said was one of the common trees above 1500 feet towards the head of the Arima Valley (i.e., on the route of the Blanchisseuse Road), I was able to show him Mr. Broadway's specimens and impressed on him the interest of this tree as an undescribed entity. In April, 1960, Dr. Snow wrote that the *Dacryodes* was fruiting abundantly, and in the same month both he and Mr. R. S. Ayliffe, of the Trinidad Forest Department, made fruiting collections in the Arima valley, the former at 1500 feet, the latter at 9 miles on the Blanchisseuse Road at 1800 feet and thus not far from Mr. Broadway's locality. It was tantalising that flowers were still not collected but, after further appeals to the Trinidad botanists, I at last received excellent fresh flowering specimens (later supplemented by spirit and dried material) which were most kindly sent by air by Mr. R. Nichols. This material had been

[1] Continued from Kew Bull. **18**(2): 314. 1965.

[2] It is with regret we record the sad and unexpected death of Mr. Sandwith which occurred, after a very brief illness, on May 7, 1965.

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collected by Messrs. M. Bhorai and R. Ramkissoon from a single tree with male flowers in forests of the Blanchisseuse Road at 9 miles, and it is clear from the notes that their tree and those of Messrs. Broadway and Ayliffe were within 1-1½ miles of each other, while Dr. Snow's tree was not far distant.

Meanwhile, in 1957 (in "Tropical Woods," no. 106: 46-65), Dr. José Cuatrecasas had published a careful and valuable account of the American species of *Dacryodes* with a distribution map, raising the number of known representatives from 2 (*D. excelsa* and *D. peruviana*) to no less than 15, of which 10 were new species described from single collections scattered over northern South America, from the Pacific coast forests of Colombia and Ecuador to the lower slopes of Mt. Roraima on the Venezuela-British Guiana boundary and the forest reserve at Belém, at the mouth of the Amazons. Some of these specimens were found by him in the covers of others genera of *Burseraceae* in the United States National Herbarium, and I have had a similar experience at Kew.

The distinctions between the taxa recognized by Dr. Cuatrecasas are finely drawn and his key, since "the useful characters for identification are not always present in the specimens," is based mainly on the size, shape and texture of the leaflets and the size of the drupes. He claims that such characters are taxonomically reliable, though often difficult to translate into descriptions, but this claim seems rather naïve when one considers the notorious variability, due to so many causes, in the size, shape and texture of the foliage of different individuals (or even of the same individual) of the same species of large tropical trees, and the fact that most of Dr. Cuatrecasas's species have been described from only one or two gatherings (each of them from a single tree?). A glance at the extensive herbarium material of *D. excelsa* from the West Indies shows a considerable range of variation in the size, shape and texture of the leaflets of that species, and in the length of their acumen: some of the examples with larger, thinner leaflets and a longer acumen were possibly collected from young trees or younger untypical shoots, but there is no evidence of this from notes on the labels. The species are dioecious with unisexual flowers and, up to the present, of the American representatives, presumably only *D. excelsa* is known from collections of flowers of both sexes and of fruits. The inflorescences and small green flowers of these species seem superficially very alike.

I cannot myself fit the Trinidad material into any of the species described by Dr. Cuatrecasas or defined in his key. I think that, on account of the very similar fruits, it comes nearest to *D. excelsa*, which does not reach Trinidad, and to *D. belemensis* Cuatr., of Belém, Pará. It differs from both in the more numerous (usually 4-5) pairs of leaflets, and from *D. excelsa* it further differs in their narrow shape with more numerous main lateral nerves, and in the much shorter pedicels of the flowers, while *D. belemensis* according to the description has more coriaceous and more shortly acuminate leaflets which are puberulous beneath, and narrow drupes. Many of the Kew specimens of *D. excelsa* have very shortly or imperceptibly acuminate leaflets of a much thicker texture than that of the Trinidad tree. Finally, *D. paraensis* Cuatr., from the State of Pará, Brazil, clearly differs from it in the membranous-chartaceous 2-3-jugate leaflets and much smaller fruits;

while *D. glabra* (Steyermark) Cuatr., of the mountains of Estado Bolívar Venezuelan Guiana, is even more distinct on account of its small, ovate or elliptic-ovate, 2-jugate leaflets with less numerous lateral nerves and, again, very small fruits.

This being so, and in sympathy with Dr. Cuatrecasas's apparent hesitation in presenting his synopsis of species (or, should we say, specimens?) of a genus which have been collected, for the most part, in a haphazard way and recognized only long afterwards, I feel little compunction in describing the now well-collected, though still incomplete, material of the Trinidad tree as follows:

Dacryodes **trinitensis** Sandwith, sp. nov.; *D. excelsae* Vahl affinis, foliolis 3-5-jugis pro rata longis ac angustis saepius tenuioribus atque longius acuminatis, nervis primariis utroque costae laere 10-14-jugis, pedicellis brevioribus differt. *D. belemensis* Cuatr. ex descriptione ob foliola firme coriacea 2-3-juga brevius acuminata subtus plusminusve puberula, necnon drupam angustiorem distinguitur.

Arbor satis excelsa, ramulis summis teretibus sulcatis lenticellatis pallide brunneis vel siccitate albo-flavescentibus oculo nudo glabris sed sub lente forti minutissime papilloso-puberulis. *Foliorum* petiolus 2.5-7 (vulgo 4.5-6) cm longus; internodia rhacheos 1.5-4.5 cm longa; petioluli tenues, supra canaliculati, 4-11 mm longi; foliola imparipinnata, 3-5-juga, lanceolata, elliptico-lanceolata, anguste oblongo-elliptica, vel infima nonnunquam ovata et foliolum terminale nonnunquam obovatum vel obovato-ellipticum, apice in acumen apice ipso obtusum 0.8-1.5 cm longum sensim attenuata, basi obliqua cuneatim attenuata vel obtusa vel etiam (praesertim latere superiore) rotundata, 6-14 cm longa, 2-4.7 cm lata (ima foliorum summorum nonnunquam 3-4.5 cm × 1.4-1.8 cm), glabra, integra, firme chartacea usque satis tenuiter coriacea, costa nervisque primariis utroque ejus latere 10-14 a sese 0.5-1.5 cm (rarius usque 2 cm) sejunctis sursum arcuatis supra subplanis vel prominulis subtus prominentibus, rete venularum intricatissimo utrinque prominulo vel in exemplis coriaceis supra subimmerso ac obscuro. *Inflorescentia* mascula pyramidalis, e basi ramosa, 8-12 cm longa, statu vivo pallide viridis, oculo nudo glabra sed sub lente forti minutissime furfuraceo-puberula; bracteolae ovatae, acutae, circiter 0.75-1 mm longae, 0.75 mm latae; pedicelli circiter 1-2 mm tantum longi. *Flores* masculi tantum visi, virides. *Calyx* leviter cupularis, 1.2 mm altus, 2.5-3 latus, glaber, margine truncato vix sinuato denticulis vix cernendis. *Petala* 3, rarius 4, quam calyx pallidius viridia, ovata, acuta, apice brevissime inflexo leviter cucullata, 2.5 mm longa, 1.8-2.2 mm lata, coriacea, glabra. *Stamina* filamentis 0.5 mm longis glabris; antherae 1 mm longae, circiter 0.5-1 mm latae, apice minute apiculatae. *Ovariodiscus* annulari-conicus vix 1.5 mm altus, sulcatus, basi quinquangulatus fere ad 2 mm latus. *Drupa* ovoideo-ellipsoidea vel ovoidea, 1.8-2.5 cm longa, 1.3-1.6 cm lata, epicarpio in vivo viridi sed siccitate ochraceo-olivaceo vel nigrescente atque more generis nitidulo laxe reticulato-rugoso, maturitate tenui atque facile detersili; nucula cum endocarpio corneo, tota 1.7-2.1 cm longa, 1.3-1.4 cm diametro, bilocularis, loculo altero minimo vacuo altero magno seminifero.

Trinidad. Northern Range, Arima Valley, Blanchisseuse Road, 9th milepost, in rain forest at 1800 ft, tree 70 ft, fl green, May 25th 1963, *M. Bhorai* & *R. Ramkissoon* (field no.

B. 819) in *Trin. Herb. 18586* (K, holotype); *ibid.*, fr April 5th 1960, *R. S. Ayliffe* in *Trin. Herb. 16498* (K); *ibid.*, 10½ mile-post, fr Jan 16th 1925, *W. E. Broadway* 5525 (K); *ibid.*, forest in 1500 ft, large tree, fr April 1960, *D. W. Snow s. n.* (K).

The late W. E. Broadway's register of his collections, preserved at Kew, records that a duplicate of his no. 5525 was sent to the British Museum Herbarium.

In my description I have adopted the term *ovariodiscus,* as used by Prof. H. J. Lam in his paper on the morphology of the *Burseraceae,* in Ann. Jard. Bot. Buitenzorg **42** (1932), see pp. 129-130 and *tt. xi* & *xii,* to cover the fusion of the disk with the rudimentary ovary in the male flower.

Dr. Snow succeeded in growing seedlings of this species from seeds dropped by the Oilbirds in the Oilbird cave at 1200 feet in the Arima Valley area. A specimen of these is in the Kew Herbarium, showing an apical pair of opposite trifoliolate leaves about 8 cm long with membranous, lanceolate or elliptic-lanceolate leaflets 3.5-5 $\times$ 1.2-1.7 cm and very conspicuously and narrowly acuminate for 1-1.2 cm. The entire plant, about 22 cm high, is pubescent with hairs extending even to the main nerves of the leaflets, and is also clothed with copious reddish brown, sessile glands.

Dacryodes trinitensis features (as *Dacryodes* sp.) as one of the most important food trees of the Oilbird in the Arima Valley in Dr. Snow's recently published paper on the natural history of the Oilbird in Trinidad, Part 2 (Population, Breeding Ecology and Food), in Zoologica **47**(4): 199-221 (1962). He points out (p. 220) that this species is the "Gommier Montagne" of Dr. J. S. Beard's "The Natural Vegetation of Trinidad" (Oxford Forestry Memoirs, no. 20, 1946). Dr. Beard lists "Gommier Montagne" as "Protium sp., unidentified," a member of the Lower Montane Rain Forest formation, in the *Byrsonima spicata-Licania ternatensis* association (see pp. 33, 114, 120 & 141). Dr. Snow tells me that he knew of one tree growing as low as 500 feet in the Arima Valley. He also found one tree at 1000 feet on the north side of the Northern Range on the Blanchisseuse Road. He adds that, as *Dacryodes* seeds are always found in other Oilbird caves elsewhere in the Northern Range, trees of this species are doubtless widely distributed.

The seeds of the *Dacryodes* are described and figured by Dr. Snow on pp. 208 (Fig. 8) and 209 of his paper. He states that the trees fruited in alternate years in the period of his study (1958-1962): the fruits, borne in large bunches, ripen slowly and irregularly, and it is the non-succulent pericarp with high food-value which attracts the Oilbird and is digested, the seed being regurgitated intact. The bird, he further suggests, is guided to this aromatic tree and to other "spicy" species with suitable fruits by its sense of smell.

I am most indebted to him for the important part he has played in launching *Dacryodes trinitensis,* not merely as a species new to science and to the flora of Trinidad, but as a very interesting tree in the field of general biology.

NOTES ON SEASHORE VEGETATION OF KENYA

By Jonathan Sauer

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For plant species, as for human groups, the East African coast is an ancient meeting ground of maritime invaders and continental natives. The historically diverse floristic elements have deployed through a variety of coastal habitats: intertidal shores of quiet alluvial estuaries and marine inlets, spray swept cliffs and dry inland ridges of emerged fossil coral, sheltered and open beaches, active and stable dunes. Superimposed on the sharp contrasts in substrate and exposure are regional rainfall gradients and local differences in artificial disturbance. The resultant intricate vegetation patterns are worthy of more study than they have yet received.

Vegetation along the temperate southeast coast as far north as Lourenço Marques has been well described (Muir, 1937; Macnae, 1963) and there is a good informal description for Zanzibar (Werth, 1901), but the mainland tropical coast is very incompletely known. Engler's classic account of African vegetation (1908-21) treats the coast of Tanganyika but for Kenya mentions only the occurrence of mangroves at Lamu. The major study of East African mangrove ecology (Walter & Steiner, 1936) is based entirely on Tanganyika. The current Flora of East Tropical Africa gives only a single Kenya locality, usually Mombasa, for each of the major mangrove species (Lewis, 1956). Finally, Birch (1963) has provided a qualitative description of part of the Kenya coastal vegetation, emphasizing climax forests and inner bushland formations on stable substrates. The rather casual observations of outpost vegetation offered here are largely complementary to Birch's study. My acquaintance with this area was incidental to a field studies of the Seychelles, conducted by Dr. William McIntire and myself. For about a week in April, 1963, while waiting for our ship to sail, and again after our return in June, we reconnoitred accessible sites within a 50 mile radius of Mombasa.

Low mangrove forest was encountered in widely disjunct patches, the most extensive fringing the maze of tidal channels near Mida, Kilifi, Mtwapa, and Mombasa. Mangrove colonies occupy mud, sand, and coral shores, flooded by brackish and by sea water, the common denominator being simply an intertidal situation sheltered from wave action. Floristically and structurally, this vegetation is identical to that described for coastal swamps of Tanganyika and Zanzibar. The dominant species of *Rhizophora, Ceriops, Bruguiera Sonneratia,* and *Avicennia* (Table 1) are identical to those we found in Seychelles swamps. They all produce seedlings capable of long-range dispersal by ocean currents and have enormous natural ranges in the Indian and Pacific Oceans (Schimper, 1891). Presumably they originated in the Indo-Malayan region, the present center of diversity of these and other paleotropic mangroves (Hou, 1958). Closely related precursors are now being traced through palynological work in Tertiary swamp deposits of Borneo

Ann. Missouri Bot. Gard. **52**(3): 438-443. 1965.

Table 1. Members of seashore vegetation in sites studies.[1]

Pandanaceae
- *Pandanus kirkii* Rendle

Gramineae
- *Lepturus repens* (Forst.) R. Br.
- *Sporobolus virginicus* (L.) Kunth

Cyperaceae
- *Cyperus maritimus* Poir.

Palmae
- *Cocos nucifera* L.
- *Hyphaene coriacea* Gaertn.

Liliaceae
- *Dipcadi longifolium* (Lindl.) Bak.

Taccaceae
- *Tacca pinnatifida* Forst.

Orchidaceae
- *Eulophia petersii* Rchb. f.

Casuarinaceae
- *Casuarina equisetifolia* L.

Chenopodiaceae
- *Suaeda monoica* Forsk.

Amaranthaceae
- *Aerva lanata* (L.) Juss.

Lauraceae
- *Cassytha filiformis* L.

Capparidaceae
- *Capparis cartilaginea* Decne.
- *Cleome strigosa* (Boj.) Oliv.

Caesalpinaceae
- *Caesalpinia bonduc* (L.) Roxb.

Fabaceae
- *Canavalia cathartica* Thou.
- *C. maritima* (Aubl.) Thou.
- *Crotalaria bagamoyoensis* Bak. f.
- *Desmodium umbellatum* DC.
- *Rhynchosia velutina* Wight & Arn.
- *Stylosanthes hamata* (L.) Taub.
- *Tephrosia purpurea* (L.) Pers.

Zygophyllaceae
- *Tribulus cistoides* L.

Euphorbiaceae
- *Dalechampia scandens* L.

Celastraceae
- *Cassine schweinfurthiana* Loes.

Sapindaceae
- *Dodonaea viscosa* Jacq.

Rhamnaceae
- *Colubrina asiatica* (L.) Brongn.

Vitaceae
- *Cissus* sp.

Tiliaceae
- *Grewia glandulosa* Vahl

Malvaceae
- *Hibiscus tiliaceus* L.

Sonneratiaceae
- *Sonneratia caseolaris* (L.) Engl.

Rhizophoraceae
- *Bruguiera gymnorhiza* (L.) Lam.
- *Ceriops tagal* (Perr.) C. B. Rob.
- *Rhizophora mucronata* Lam.

Combretaceae
- *Terminalia catappa* L.

Sapotaceae
- *Sideroxylon inerme* L.

Oleaceae
- *Jasminum mauritianum* Boj. ex DC.

Asclepiadaceae
- *Pergularia extensa* (R. Br.) N. E. Br.

Convolvulaceae
- *Ipomoea pes-caprae* (L.) Sweet

Boraginaceae
- *Cordia somalensis* Bak.
- *Heliotropium gorinii* Chiov.

Verbenaceae
- *Avicennia marina* (Forsk.) Vierh.
- *Clerodendrum glabrum* E. Mey.

Acanthaceae
- *Asystasia gangetica* (L.) T. Anders. in Thwaites
- *Justicia flava* Vahl

Rubiaceae
- *Guettarda speciosa* L.
- *Oldenlandia amaniensis* Krause
- *Psychotria punctata* Vatke

Goodeniaceae
- *Scaevola plumieri* (L.) Vahl

Compositae
- *Launea bellidifolia* Cass.
- *Tridax procumbens* L.
- *Wedelia biflora* (L.) DC.

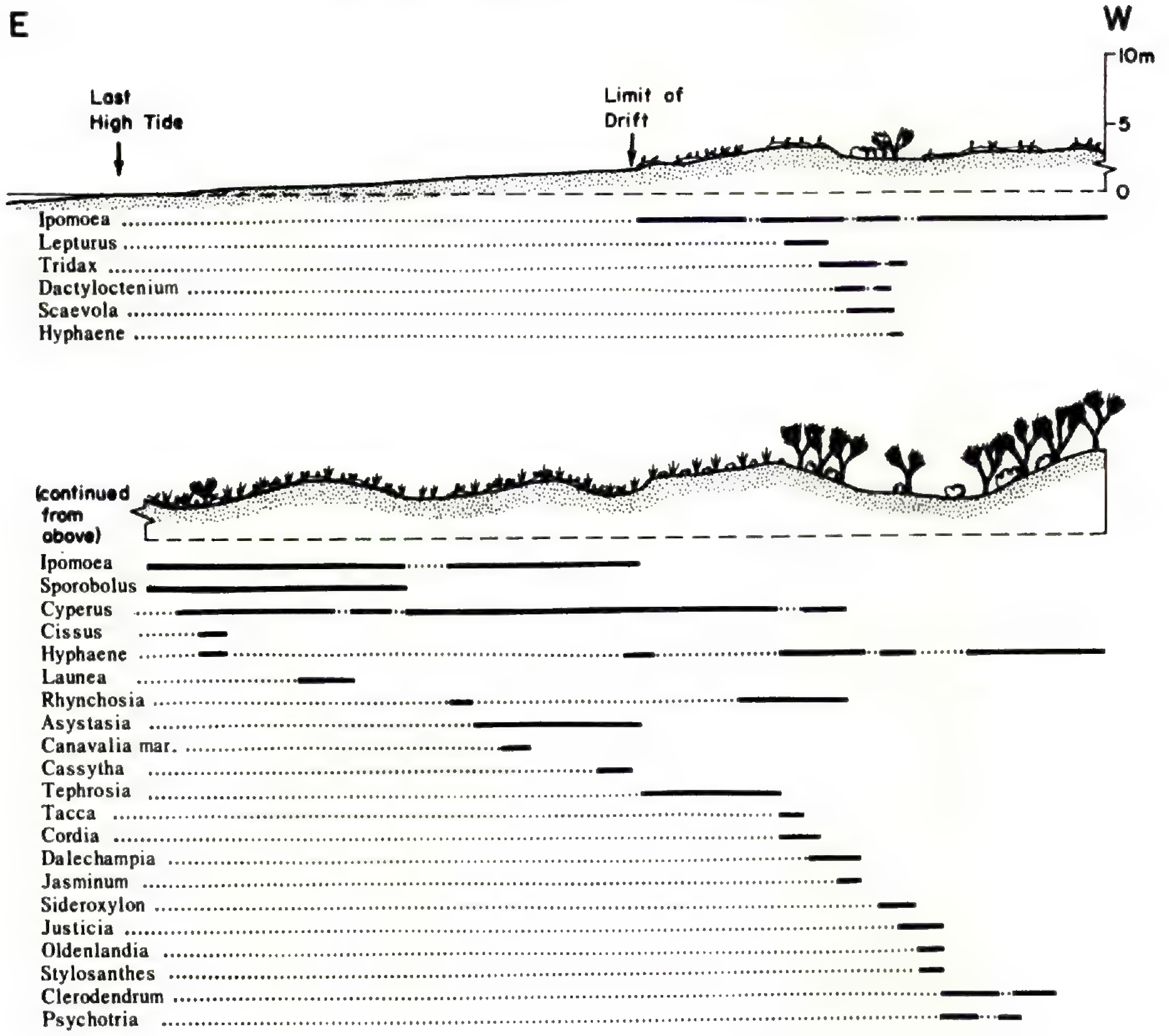
[1] Collections made of all species except the pandanus and palms, mainly deposited in EA and WIS, duplicates of some in F, MO, UC.

(Muller, 1964). In the history of human activity on the Kenya coast, mangroves have played a long and important role. Mangrove exploitation for tanbark and timber is the traditional livelihood of the Bajun Islanders of the Lamu region. Since ancient times, Arab house construction has depended on mangrove poles brought by dhows from Lamu and the Tana delta in Kenya and from the Rufiji delta in Tanganyika (Rawlins, 1957; Villiers, 1940).

The dry coastal vegetation is floristically distinct, with only a few mangrove

Plate A. Fig. 1-2. Views northward and southward at site of transect shown in Fig. 1, June 16, 1963. Doum palms (*Hyphaene*) forming scattered outposts in active dunes and solid thickets in stabilized dunes. Fig. 3-4. View northward at site of transect shown in Fig. 2, April 24, 1963 and June 15, 1963. The change in luxuriance of the outpost vegetation in the interim between the pictures is due to increased wave attack with the onset of the southeast Trades.

associates such as *Hibiscus tiliaceus* and *Suaeda monoica* ranging into supratidal habitats. The great Pleistocene coral reef, generally about 15 m above present sea level, is a conspicuous feature of the coastal landscape in Kenya, just as in Tanganyika and Zanzibar. Where it is now being cut by the sea, as at Mtwapa, Nyali, and south of Likoni, the roughly pitted spray zone bears a prostrate, evergreen scrub dominated by a spiny caper bush. This is *Capparis spinosa* in the broad sense, usually segregated as *C. cartilaginea* in African floras. We found very similar caper bushes on emerged coral in the Houtman Abrolhos Islands off Western Australia (Sauer, 1965). A closely related variety in Timor and certain Pacific islands is suspected of having escaped from early Portuguese introductions (Jacobs, 1960). Starting with Vasco da Gama's first voyage, Portuguese ships regularly called at Malindi or Mombasa en route to India, so the suspicion is plausible. This species complex holds various remarkable geographic and historic patterns awaiting systematic study.



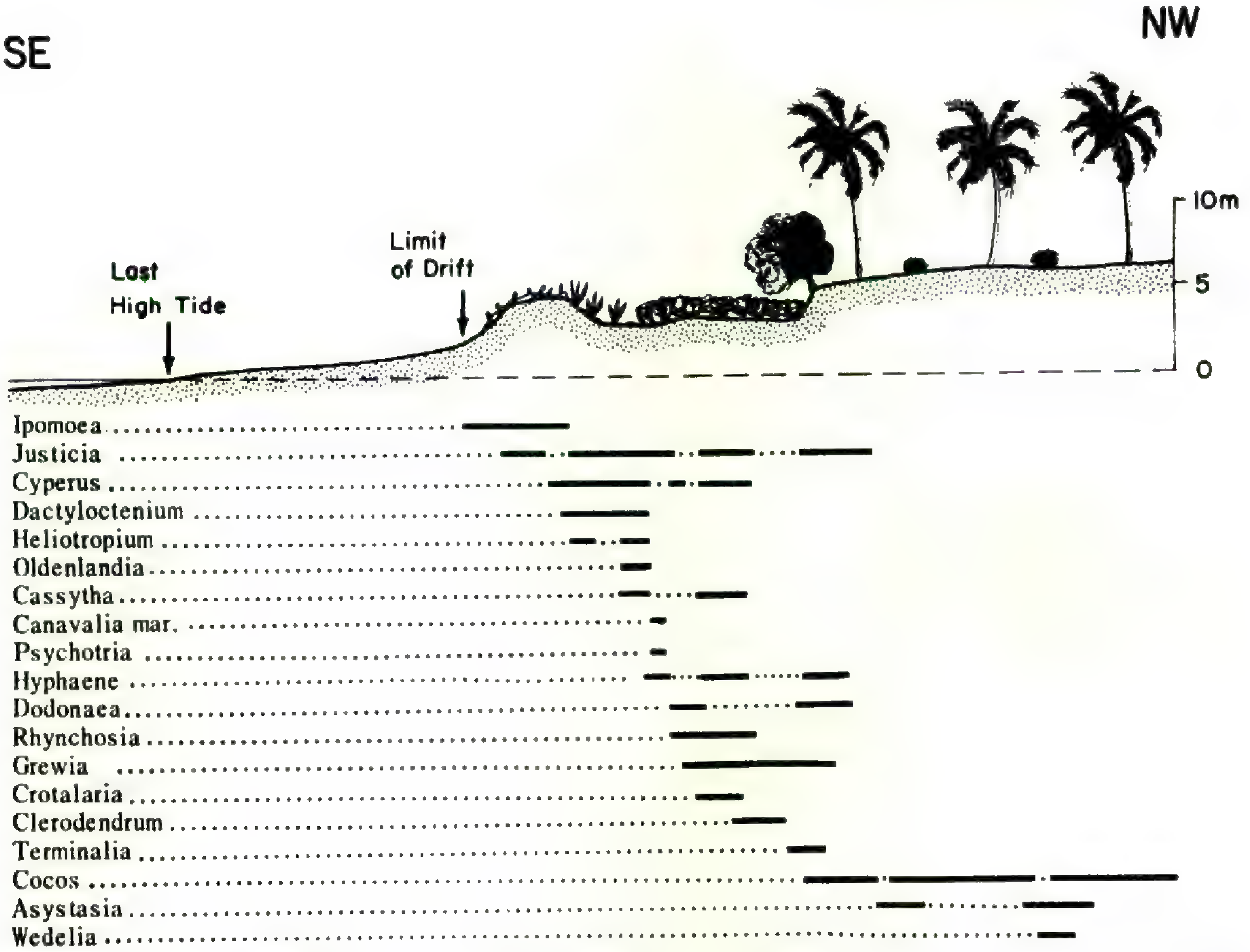


Fig. 1 (top). Transect on mineral sand beach exposed to heavy surf and spray, between Malindi and Galana River mouth, Kenya. Fig. 2 (bottom). Transect on partially reef-protected coral sand beach at Nyali, nr Mombasa, Kenya. (Horizontal and vertical scales identical).

Weathered or sand-covered coral ridges behind the spray zone bear a complex evergreen scrub vegetation, dominated by peculiar native species (Birch, 1963). Much of this inner coastal zone has been cleared for garden patches or plantations of *Cocos* and *Casuarina*. It is obscure how and when these trees reached East Africa. Both had wide prehistoric ranges in the Indo-Pacific region, partly artificial and party natural. The *Casuarina* is less well adapted for long-range sea dispersal than the coconut. Ancient Malay voyagers may be responsible for its early presence in Madagascar. There is historical evidence that coconuts were growing on the East African coast in the 1st Century A.D. (Hourani, 1951). Islands near Lamu on the Kenya coast were said to be celebrated for their coconuts in the 13th Century (Freeman-Grenville 1962). The classical Arab sailing ship was carvel built of coconut planks sewn together with coir, rigged with coir cordage, often with coconut trunk masts and coconut leaf fiber sails (Hourani, 1951).

The pioneer vegetation of storm beaches and active dunes is different from that of the coral. The outpost fringe is formed by sprawling beach vines, mostly *Ipomoea pes-caprae*, prostrate grasses, sedges, and scattered low herbs. These plants undergo perpetual micromigrations as wave reach changes with monsoonal wind shifts and with seasonal tide levels (Plate A: Fig. 3-4). The outpost zone is much wider on beaches open to heavy surf than where there is a reef offshore (Fig. 1-2) but the flora is very uniform on all the beaches seen, in spite of differences in exposure, kind of sand, and rainfall. More intensive distribution studies in other areas, involving many of the same species, also indicate little sensitivity to coastwise variation in these factors (Sauer, 1961, 1965). In the beach and active dune flora, slightly over half the species have wide Indo-Pacific ranges, like the mangroves, or are pantropical. A few cosmopolitan species, such as the *Dalechampia* and *Dodonaea* (Table 1) present migrational puzzles and a few weedy ones, such as the *Tribulus* and *Tridax*, are probably artificially dispersed, but the great majority are adapted for regular long-range dispersal by ocean currents. These sea-dispersed species, particularly the pantropical ones, tend to concentrate in the zone closest to the sea. Only a few African species, notably the endemic coastal *Cleome*, grow as extreme outpost plants. Native species become predominant back where the pioneer fringe of woody plants begins to colonize and stabilize accretion beach surfaces and outer dunes (Fig. 1-2). Many of these African pioneer species, including the conspicuous *Hyphaene* or doum palm, are not strictly coastal but range inland in open habitats. The predominance of African species in the back beach and outer dune zone may be attributed to superior adaptation to the local habitat rather than default of seaborne competitors. The Indo-Pacific strand flora includes a wealth of shrubs and trees which occupy comparable sites in oceanic islands, including the Seychelles. Their drift seeds regularly reach the East African coast in sound condition and scattered mainland colonies are known for many species (Muir, 1937). On the Kenya beaches a few Indo-Pacific shrubs and trees were encountered, e.g. *Colubrina, Terminalia, Guettarda,* and *Scaevola,* but they are quantitatively unimportant among the native woody plants. About a dozen of the wide-ranging Indo-Pacific species have closely related congeners on this coast or

its hinterland, suggesting possible ancient interchanges between the maritime and continental floras.

ACKNOWLEDGEMENTS

The field work was supported by the Coastal Studies Institute of Louisiana State University with funds provided by the Geography Branch, Office of Naval Research. For help with identifications I am grateful to B. Verdcourt and D. Napper of the East African Herbarium, Nairobi, and to Robert E. Woodson of the Missouri Botanical Garden.

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THIS REMARKABLE KENTUCKY BLUEGRASS

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Bob Woodson had a particular "pet," butterfly weed, *Asclepis tuberosa,* on which he lavished many years in study of its populations. So, for this commemorative issue, it is perhaps relevant for me to muse about a lawnsman's "pet," Kentucky bluegrass *(Poa pratensis),* certainly no stranger to the pages of the Annals (viz. 2, 5). Because bluegrass is one of the outstanding lawngrasses, I have had occasion in recent years to watch its performance rather closely, hoping to relate its population dynamics to the new ecology of suburbia.

Considering *Poa pratensis* to embrace wide-ranging populations found in all states of the U.S.A. (fide Hitchcock, 1), here is a truly remarkable taxon, and one considerably more complex than butterfly weed. European taxonomists have tended to split *Poa pratensis,* but broadly considered the species is ubiquitously circumboreal.

There has long been interest in the exceedingly complicated heredity of Kentucky bluegrass, largely apomictic and highly polyploid. Cytogenetic studies were made by Brown about 1941 (2). Very extensive work was done in Wisconsin from the mid 1930's through the early 1950's, chiefly by E. L. Nielsen and D. C. Smith (3). These and other works show how involved is *Poa pratensis,* even to uncertainty about its diploid chromosome number (a base number of 7 seems to hold, but published chromosome counts reach 147 and higher). Perhaps Barnard (4), discussing grass cytogenetics, summarizes as well as possible: "*P. pratensis* has demonstrated its ability to absorb genomes from many different sources and occasionally give rise to valuable new apomictic segregates. This may explain the polymorphism characteristic of this apomictic complex, and account for its adaptability, and wide distribution throughout the Northern Hemisphere."

With Kentucky bluegrass already so widely treated in the literature, one might suppose that there is relatively little novel to report about it. Nonetheless, most publications have dealt with its physiologic responses or genetic pecularities, or, among agriculturists, with yields and management. One of the relatively few attempts to examine Kentucky bluegrass holistically is that of Etter (5).

It is not my purpose to review the literature on Kentucky bluegrass, which would be a volume unto itself. Rather I will record certain observations made on "wild" (volunteer) stands of "natural" (unselected) *Poa pratensis,* at numerous locations through the Midwest (Kentucky; Missouri-Iowa; Minnesota-Dakotas), over a period of several years. Until very recently most of the Kentucky bluegrass lawn seed was harvested from such stands. Therefore, whether distinctive ecotypes had evolved was of some importance, lest they be only locally or narrowly adapted.

The Lawn Institute, in checking this out, arranged for numerous known-origin seed samples to be planted side by side in various parts of the country. The tests

Ann. Missouri Bot. Gard. **52**(3): 444-451. 1965.

Table 1. Sods forced greenhouse. Figures in parenthesis indicate range of variability. Units of measurement are 1/32nds of inch.

	number "clones"	*shoots/ linear 2"*	*mean width 2nd panicle lf.*	*"clone" extremes*	*number samples*	*mean width all vegetative leaves*	*"clone" extremes*	*number samples*
Minnesota	36	6.36 (8-5)	3.21 (4-2)	2.5-3.8	81	2.91 (4-2)	2.5-3.3	360
North Dakota	30	6.37 (8-5)	3.08 (4½-2)	2.5-3.6	86	2.87 (4-2)	2.3-3.6	300
South Dakota	42	6.50 (7-5)	3.31 (4½-2)	2.8-4.0	283	2.94 (4-2)	2.6-3.4	420
Iowa	42		3.53 (5-2)	2.6-4.7	258	3.31 (5½-1½)	2.3-4.8	420
Missouri	44		3.37 (6-1½)	2.0-4.3	154	3.27 (5½-2)	2.4-4.8	450
Kentucky	20	7.45 (9-5)	3.50 (7½-2)	2.6-5.8	75	3.21 (5-2)	2.4-4.5	200

Table 2. Mean leaf width of sods of Table 1, 3 months after planting out, mowed 3". Figures based on 200 measurements. Mowed regularly at 3 inches.

Source	*at April planting*	*July (after 3 mo.)*
Minn.-Dakotas	2.91	2.91
Iowa-Missouri	3.29	3.05

proved rather conclusively that seed harvested in any area, when adequately started in another, gave performance comparable to other sources, including local ones.[1] Occasional immediate differences, such as in rapidity of germination or seedling vigor, are largely non-genetic (but of mechanical or environmental derivation), and vary from lot to lot. Seed lot quality is much influenced by harvesting and processing, and even by the weather (comparing one year with another). Certainly heavier fractions of seed, properly cured and stored, provide better germination and greater seedling vigor, hence often a better stand. Thus, although one can presume local ecotypes (as from high vs. low ground), there is great adaptability in the mixed population (bag of seed containing all such ecotypes) as it comes to market.

More surprising than wide adaptability is natural bluegrass' unusual flexibility, such that it may change morphologically with the habitat. In as little as three months, sods from widely divergent habitats, presumably representing such distinctive ecotypes as were there, molded towards a norm when planted side by side on our test grounds. Ahlgren, Smith & Nielsen (6) pointed out years ago, with bluegrass "grown in small plots there is a marked tendency for original differences between most strains to become less pronounced as seedings increased in age." And Nissen reportedly observed in Norway a lack of significant correlation between collection locality and a number of morphological characteristics.

To further examine this flexibility, sods of natural Kentucky bluegrass in 6-inch squares were gathered from many marked locations and assembled in central Ohio. These, of course, are not truly clones, but clone-like do perpetuate a given sod complement. A number of the collection sites were visited several times, most of them at least once in autumn and several springs. It is difficult to make meaningful

[1] Only occasionally was there hint of better performance from local strains rather than from distant ones, this towards the margins of what could be considered good bluegrass country. Comparative performance is hard to measure, and if there was any significance it seemed to lie more with debilitation of northern ecotypes moved southward (to latitudes of Tennessee and Missouri), rather than the reverse.

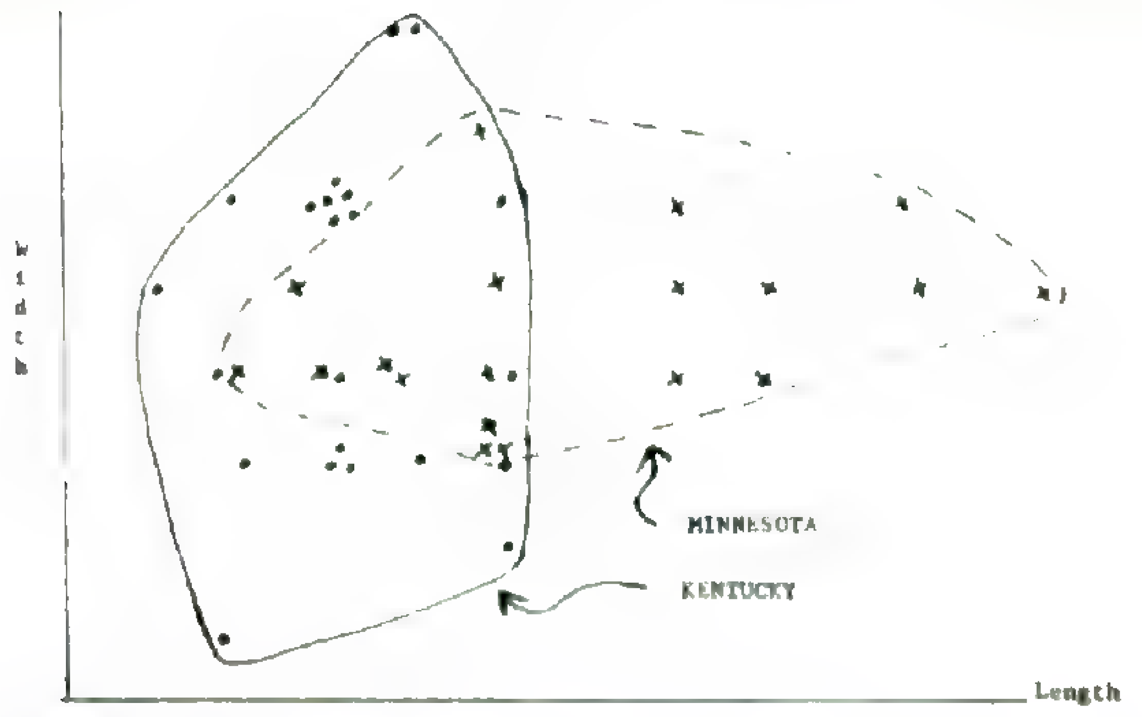

CHART 1—Comparison of the number 1 (tip) leaf on non-flowering culms of Kentucky bluegrass, in Kentucky as contrasted with Minnesota. The more extreme (longer leaf) measurements for Minnesota are those from the northern part of the state; those nearer like Kentucky are from the southern part.

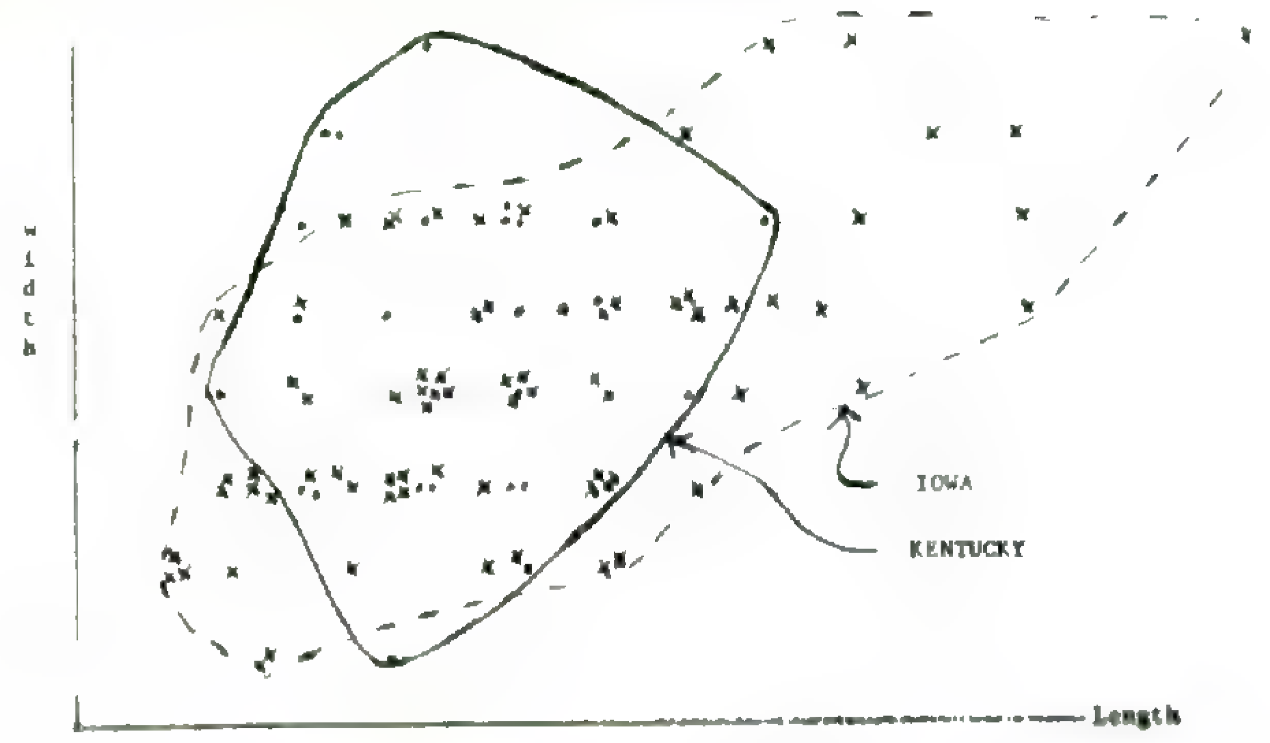

CHART 2—Comparisons of the number 2 leaf (second from tip) of non-flowering culms of Kentucky bluegrass, from Kentucky and Iowa. There's a great deal of overlap, but a tendency in Iowa for leaves to become longer, and then show less variability in width.

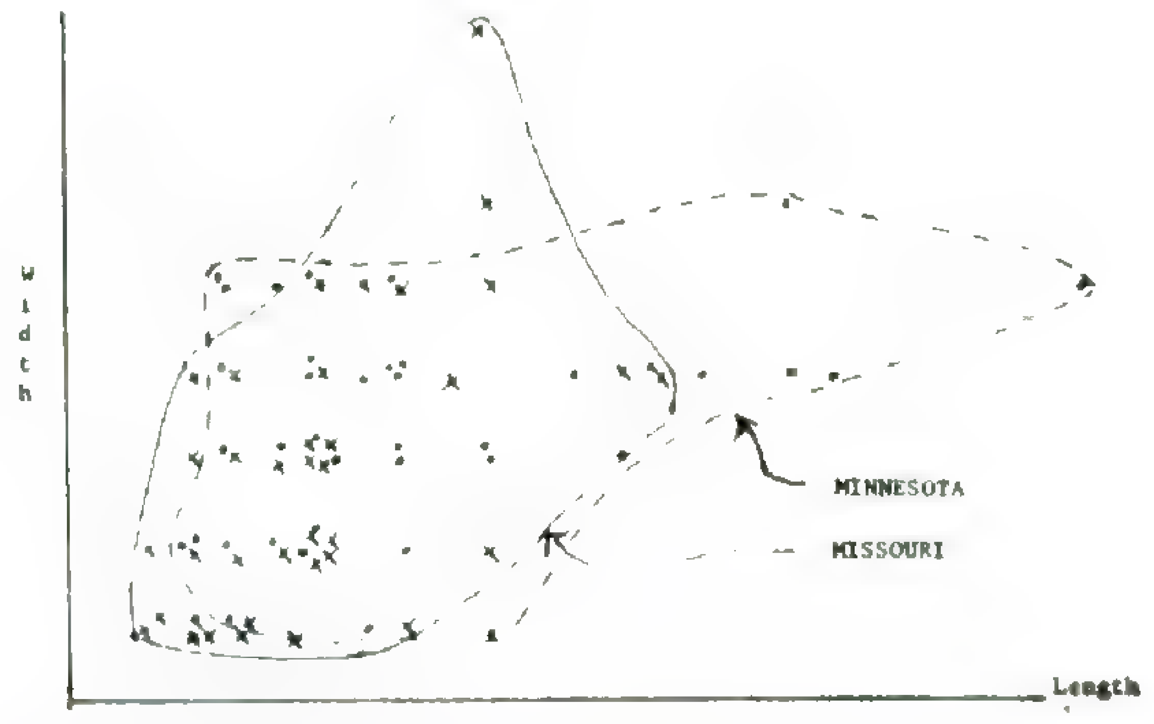

CHART 3—Comparison of leaf 3 (third from tip), on non-flowering culms, of Kentucky bluegrass from Missouri and Minnesota. The width/length spread for Missouri is not a whole lot unlike that noted for Kentucky in previous charts, and seems to differ from more northerly populations in the same general way (if not to the extent) that was the case when comparing Kentucky grass (Chart 1).

CHART 4—Comparison of the second panicle leaf, on Kentucky bluegrass from Kentucky and from Minnesota. Again, the extremes in length for Minnesota are from the northern part of the state (viz. Chart 1).

CHART 5—Comparison of the second panicle leaf of Kentucky bluegrass from Kentucky and from Missouri. It appears that the trend manifest for Minnesota in Chart 4, is already indicated in Missouri.

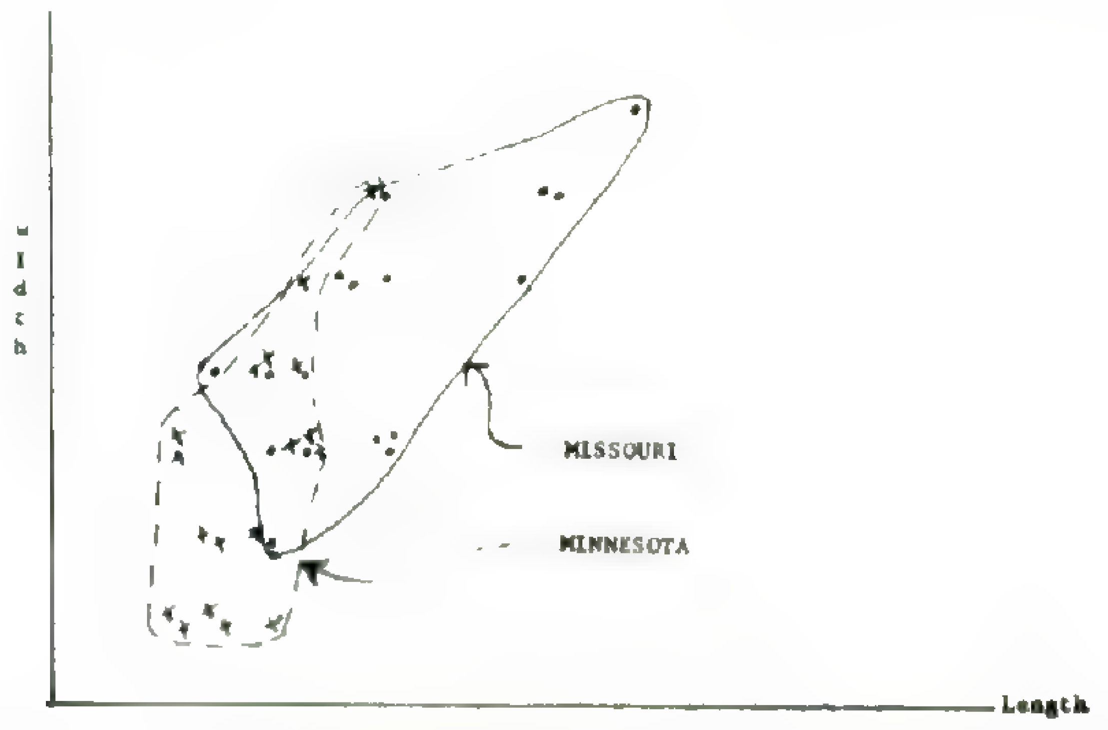

CHART 6—Comparison of the tip (flag) leaf on young panicles of Kentucky bluegrass from Missouri and Minnesota. Although Minnesota flags average shorter, there is perhaps greater genetic restriction.

phenotypic records of a heterogeneous population, so a simple leaf width measurement was settled upon, one of the characteristics used by Bär (7) and others in comparison.

Data was reported to the Botanical Society at the AIBS meetings at Stanford University in 1957, under the title of "The Remarkable Plasticity of Bluegrass *(Poa pratensis)*." Because of practical difficulties in assembling numerous sods from distant areas, because human judgment is not precise in selecting comparable leaves for measurement (equivalent stage of maturity), and because the measurements were made fairly grossly with a ruler, no claim is made for statistical significance in the figures. Nevertheless, Tables 1-4 do suggest average populational differences. Likewise, scatter-diagrams, samples of which are included as Charts 1-6, suggest a broader and somewhat differing gene pool in certain locations as compared to others. Kentucky, probably an early center for dispersal of bluegrass into the Midwest and northward, seems to have its bluegrass more diversified than the newer bluegrass populations that have colonized northern fields more recently (viz. Minnesota; upon abandonment from cultivation after World War II). This conclusion fits nicely the Vavilovian concept of dispersal of more restricted genotypes from a variable center of origin.

Regional differences in the field are often dramatic. The tussock habit of Kentucky bluegrass north and west from approximately Aberdeen, South Dakota is notable. There, and on some of the sandy soils of old Lake Agassiz (Red River Valley, North Dakota) the grass is highly untypical of that in the lower Midwest. The plants are widely spaced, in discrete clumps, rough and siliceous to the touch, unusally erect (not tending to spread and flop), the leaf margins often inrolled (looking more like a fine fescue than a bluegrass). Panicles are compact, and as seed harvesters well know, seed from northerly regions tends to be heavier and less chaffy than that in the South. Yet such sod planted in Ohio turns almost indistinguishable from Ohio sod! The uncommon field appearance must in large measure be adaptation of a flexible genetic base to the local environment—perhaps harsher, more desiccating; the soil more nearly virgin, undepleted; with meadowing practiced on northern grass, pasturing on southern; etc.

Such differences in the field can be verified simply by shoot counts. The number of culms per square foot of sod (late September and early October) averaged about 630 for Kentucky-Missouri-Iowa, only 440 for South Dakota—North Dakota —Minnesota (based upon scores of samplings). In spring a series of sods in Kentucky averaged about 1200 shoots per square foot, while in South Dakota (at an

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CHARTS 1-6. Scatter-diagrams comparing width/leaf measurements for equivalent leaves on both flowering and non-flowering culms, for the states indicated on the individual charts. Other leaves, and other state comparisons, fall generally within the trend noted in these six examples. The variable width and comparatively modest leaf length exhibited by Kentucky populations, trends gradually to restriction in width and greater length, westward and northward into Missouri, Iowa and Minnesota. This is essentially the progression of settlement, and it may be that especially adaptive genotypes (for prairie conditions) moved from an original center near the Ohio valley into newly cultivated lands northwest. The progression is still moving westward, with Kentucky bluegrass showing up in western Nebraska, Wyoming, and other areas where none was known some years ago.

estimated equivalent stage of development) the count was only 680, in Minnesota 570, and in North Dakota 470. Obviously, density peters out northwestward, for whatever the cause.

But as Rollins (8) points out, one of the first tasks in study of a species is to find out which part of the phenotypic variation is correlated with environment, and which part is under direct genetical control. That not a great deal of this density difference is genetic, can be shown by comparison of populations receiving differing treatment in a given area. For example, in Missouri and Iowa, spring shoot count for heavily grazed pastures reached 1330, while nearby ungrazed fence rows had a shoot count of only 544. On the grazed areas there were many more shoots and leaves, but these were quite dwarfed. While I am confident that there is more bluegrass (of greater diversity) per square foot in Kentucky than in North Dakota, I do think the earlier shoot count figures are misleading chiefly because Kentucky grass is mostly grazed, Dakota grass cut for hay. We know in lawn tending that management generally overshadows varietal choice!

Let us turn to the scatter-diagrams Charts 1-6. These match leaf length against width, on a series of regional sods, taken dormant, then forced in the greenhouse. Measurements were made at early inflorescence. Both vegetative and fruiting culms were compared, with reasonable care taken to choose leaves of equivalent maturity. While there is much overlapping and variability, a general trend appears to exist. Using Kentucky grass as the base for comparison, leaves tend to be longer and less variably wide westward and northwestward, at least in younger foliage. There seems to be greater variability (a larger gene pool?) in Kentucky and in the South, than with newer populations farther north!

Mean differences in leaf width are given in Table 1. Here too, there is generally less variability, narrower leaves, in the North than in the South.

But in Table 2 we see the beginnings of conformity to a new environment. Sods of Table 1 (planted out) had leaf width measured in July, three months after the Table 1 recordings. There is some convergence.

Table 3 gives mean leaf widths the next following growing season. Here the spread is narrowed further (although the sods are not exactly those of Table 2).

Table 3. Mean leaf width of sods 2nd year after planting out. Figures in 1/32nds of inch, based on 200 leaf measurements, given in 1/32nds of inch.

Source	*mean leaf width* *July*
South (Kentucky)	3.12
South (Missouri—Iowa)	3.02
North (lower Minnesota—Dakotas)	2.96
North (upper Minnesota—Dakotas)	2.84

Table 4 compares populations (sod) started from seed from known locations. There is no logical explanation why South Dakota and North Dakota should seem so untypically different from one another, other than to point out again that what part of a harvest ends up as an individual seed lot may have a greater bearing than does region of production.

To summarize, I excerpt the abstract from my Golden Jubilee Agronomy meet-

Table 4. Inflorescence and leaf measurements of unmowed row plantings in 2nd year, from known-origin seed. Seed fractionation and measurements showed no correlation. In mm.

	mean infloresc. length	*range*	*samples*	*mean width 2nd panicle leaf*	*range*	*samples*	*mean veg. leaf width*	*range*	*samples*	*"widest" leaf mean of 3*
N. Dak.	85	(55-125)	84	3.9	(3.0-4.9)	51	2.3	(1.7-3.2)	90	5.0
S. Dak.	74	(45-100)	69	3.1	(1.9-4.5)	43	2.0	(1.2-2.8)	73	5.0
Iowa	81	(45-110)	88	3.7	(2.4-5.2)	48	2.3	(1.2-3.5)	81	5.4
Nebr.	99	(50-170)	96	3.8	(2.2-5.5)	59	2.3	(1.7-3.5)	89	6.2
Ill.	86	(65-110)	20	3.9	(2.9-5.2)	20	2.3	(1.4-3.0)	37	4.6
Ky.	86	(55-120)	44	4.2	(3.0-6.2)	25	2.5	(1.2-5.0)	74	6.3

ings paper, "Regional Adaptation in Kentucky Bluegrass:" "Compared to corn, wheat, alfalfa, and familiar crops having strains adapted to limited climatic zones, Kentucky bluegrass perhaps presents a unique example of widespread adaptability and plasticity. Phenotypic adaptation suggests an extremely flexible genotype. Kentucky bluegrass selections from as far north as Canada to as far south as Missouri and Kentucky, survive well side by side when planted in multiple environments throughout the northern two-thirds of the country. Although more diversity is evident in southern areas, the very different appearances in field and meadow is more an adaptation to soils, rainfall, and method of use than to stable genetic qualities.—" The Kentucky bluegrass phenotype appears quite laxly under genetic control.

This broad flexibility noted in *Poa pratensis* is not typical of most plants. Hanson & Carnahan (9) indicate that though cool-season grasses are usually widely adaptable, seldom are range species suitable for zones greater than 300 miles in latitude. McMillan (10) notes ecotypic differentiation in prairie grasses persisting within transplanted community fractions, with a rigidity Kentucky bluegrass does not display. In controlled climate chambers there was a deleterious sensitivity to changed environment that natural bluegrass seems unbothered by. Peacock & McMillan (11) pinpoint regional adaptation of physiological nature in mesquite, relating to photoperiod, temperature, onset of dormancy, resistance to freezing, and so on,—adaptations certainly not very fixed in natural Kentucky bluegrass.

Kentucky bluegrass' genetic "mix" evidently allows the grass a terrific range of response. This has enabled it to follow man the world around and become a dominant wherever good soil is turned. How like the world's most successful "weeds," as characterized by Harlan & de Wet (12): "Most weeds are characterized by enormous phenotypic plasticity. Under favorable conditions, a given genotype may be tall, robust, well developed and highly productive. Under unfavorable conditions, the same genotype may be minute, depauperate, living but a short time and producing only a few seeds." With wild oats, Harlan observes: "The nursery contained winter forms (of crop) which were still in winter rosette when spring forms in the same field were tall and heading out and some of the earliest varieties maturing. In the barley, these differences in growth habit were genetically controlled. But the wild oats with which the field was infested produced phenotypic

mimics of all the growth habits. When growing with winter barley, the wild oat formed a low winter rosette; in adjacent rows of spring barley, the wild oats were tall and heading out. Where the early barley was maturing, the wild oats were ripening. All stages could be seen on the same day. The capacity for phenotypic mimicry is presumably under genetic control and constitutes an excellent adaptive mechanism."

Although Kentucky bluegrass is certainly well adapted in the modern (disturbed) world, one wonders how well it might have fared in pre-historic American grassland communities had it then been in the New World? As to what causes the American grasslands, Wells (13) hypothesizes on paleobotanical grounds that the grassland provinces of central North America are relatively recent, correlated with young (Pleistocene) transported soils, flattish terrain; these features interacting with wind and fire to maintain the grassland. Nothing insurmountable here for bluegrass! Iltis (personal communication) is convinced that periodic burning is needed to retain native prairie in Wisconsin, in competition with "more aggressive" *Poa pratensis* and *Poa canadensis*. I expect, that in spite of occasional fire and desiccation, a species with such versatility as *Poa pratensis* shows, would have maintained a primeval foothold. I've seen it take hold in isolated montane valleys of southwestern Colorado, where the sole disturbance has been grazing (and trampling) by occasional roving livestock.

Kentucky bluegrass constitutes one of the world's most abundant and useful species, much studied, yet still enigmatic. How do variable chromosome number, facultative apomixis and similar attributes relate to the great success of Kentucky bluegrass? What were the ancestral diploids like, and where native? How can special traits be selected for, yet preserve the invaluable adaptability of natural Kentucky bluegrass? Useful genotypes, such as Merion and a few other cultivars, can be maintained under reasonably accurate identity by roguing the relatively infrequent sexual off-types and mutants. But such useful finds are seldom the equal of natural Kentucky bluegrass in self-sufficiency over the tremendous range that bluegrass occupies.

In any event, the ability of Kentucky bluegrass to mold easily and quickly to changed enviorment augurs well for its continued ubiquity and importance. With monoculture and "identicalness" the order of the day, versatile Kentucky bluegrass, proven to have the stuff for survival to an extent exhibited by few Spermatophytes, may have much yet to offer, practically, esthetically and as a source for additional genetic information.

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A PRELIMINARY STATEMENT CONCERNING MOSSES COMMON TO JAPAN AND MEXICO[1]

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Since it has been noted that certain genera and species of plants were common to Mexico and Asia by Matuda (1953) and Sharp (1953, 1965), it was felt that a preliminary study of mosses common to Japan and Mexico might be informative. It is interesting that identical species in the two areas are present in several categories of plants, e.g., *Mitchella repens* and *Phryma leptostachya* in the angiosperms; *Brothera leana* and *Homaliadelphus sharpii* (cf. Iwatsuki, 1958) among the mosses; *Cladonia formosana* among the lichens (Evans, 1955).

We are fortunate in having the preliminary list of mosses of Japan and its adjacent areas by Noguchi (1959) and also a preliminary list of Mexican mosses presented by Crum (1951). Although these are being modified by monographic and other studies, such as that of Robinson (1964), the changes are less at the generic level than among the species.

The moss floras of these two widely-separated areas have a total of over 300 genera in them, which at present are thought to represent over 2000 species. Of these more than one-third of the genera occur in both areas and include about 1500 species. About 150 other genera with over 300 species are present in Japan but not in Mexico. Conversely about 75 genera representing about 150 species are indigenous to Mexico but not to Japan.

It might be of interest to note the genera which have species common to the two countries. In all cases infraspecific names are ignored.

Sphagnum has about 50 species in Japan and 5 in Mexico with *S. meridense* (*S. platyphyllum*), *S. palustre*, and *S. subsecundum* common to both.

Andreaea with 4 species in Japan has 2 in Mexico with *A. rupestris* present in both.

Fissidens has 50 species in Japan and 32 in Mexico of which *F. cristatus*, *F. garberi*, and *F. grandifrons* are reported in both regions.

Garckea phascoides, found in Japan and Mexico, is of interest because of its apparently disjunctive range in America.

Ceratodon has *C. purpureus* in Japan and Mexico with 1 other species in the latter area.

Distichium is represented by *D. capillaceum* in both countries with another species in Japan.

Bryoxiphium norvegicum is present in both areas and is of unusual interest (cf. Löve & Löve, 1953).

Trematodon, with 5 species in Japan and 3 in Mexico, has *T. longicollis* common to both.

Aongstroemia has 5 species in Mexico and 1 (*A. orientalis*) in Japan which is present in the two regions.

Thysanomitrium richardi in Japan and Mexico is the sole representative of the genus in these areas.

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[1] Contribution from the Hattori Botanical Laboratory, Obi, Nichinan, Miyazaki, Japan and from the Botanical Laboratory, The University of Tennessee, N. Ser. 260.

Ann. Missouri Bot. Gard. **52**(3): 452-456. 1965.

Dicranodontium exhibits 5 species in Japan of which *D. denudatum* is the only species known in Mexico.

Paraleucobryum is represented by 2 species in Japan of which *P. enerve* is the only taxon reported from Mexico.

Brothera leana is the only species found in Japan and in Mexico.

Dicranum, well-developed in Japan (20 species), has only 7 in Mexico; *D. flagellare* and *D. scoparium* are in both.

Encalypta has 3 species in Japan of which *E. ciliata* is the only species known from Mexico.

Anoectangium, with 11 species in Japan and 8 in Mexico, exhibits only *A. compactum* in both countries.

Merceya has 2 species in Japan of which *M. ligulata* is found also in Mexico.

Weissia is represented by 8 species in Japan of which *W. controversa* is the only species in the genus in Mexico.

Gymnostomum, with 4 species in Japan, is represented by *G. calcareum* (common to both) in Mexico.

Hymenostylium recurvirostrum is the single species of the genus found in Japan and in Mexico.

Eucladium verticillatum is the only representative of this genus in Japan and in Mexico.

Trichostomum, with 7 species in Japan and 6 in Mexico, has only *T. brachydontium* common to both lists.

Timmiella anomala alone represents this genus in both areas, and is of interest because of its more disjunctive range in America.

Tortella, with 8 species in Japan and 3 in Mexico, has *T. humilis* (*T. caespitosa*) indigenous to both.

Didymodon, better represented in Mexico (13 species) than in Japan (6), has only *D. recurvirostrum* in both areas.

Barbula, with 30 species in Mexico and 11 in Japan, has *B. ehrenbergiana* and *B. convoluta* in both.

Tortula, better represented in Mexico (19 species) than in Japan (9), has only *T. ruralis* common to both.

Grimmia, more diversified in Japan (about 30 species) than in Mexico (about 15), has *G. alpicola, G. apocarpa, G. montana, G. ovalis, G. patens,* and *G. pulvinata* in both countries.

Venturiella sinensis, indigenous to Japan, is found in Texas just north of Mexico and probably occurs in the latter country; its distribution is very interesting.

Funaria, with 6 species in Japan and 7 in Mexico, has the cosmopolitan *F. hygrometrica* in both.

Pohlia, better represented in Japan (with about 30 species) and with 12 reported from Mexico, has *P. cruda, P. flexuosa* (*P. tenuiseta*), and *P. wahlenbergii* common to both areas.

Anomobryum filiforme is the only species of the genus in Japan and is among the 4 species reported from Mexico.

Leptobryum has 2 species in Japan, one of which (*L. pyriforme*) is also found in Mexico.

Bryum, with about 30 species in Japan and 25 in Mexico, has *B. argenteum, B. bicolor, B. caespiticium, B. capillare, B. coronatum,* and *B. truncorum* in both countries.

Rhodobryum roseum is the only species of the genus in both areas but Mexico has 2, and Japan 1 other species.

Mnium is represented in Mexico only by *M. rostratum, M. marginatum,* and *M. orthorrhynchum,* all of which are among the 50 species listed for Japan.

Rhizogonium has only *R. spiniforme* in Mexico but it and 4 other species are indigenous in Japan.

Aulacomnium palustre is found in Mexico, and it and 3 more species are reported from Japan.

Bartramia, with 3 species in Japan and 3 in Mexico, has only *B. ithyphylla* common to both.

Philonotis, with about the same number of species reported in Japan (10) as in Mexico (11), has only *P. fontana* in both lists.

Hedwigia with *H. ciliata* common to both countries has an additional species in Mexico.

Forsstroemia (*Leptodon*) has 4 species in Japan of which *F. trichomitria* also occurs in Mexico.

Barbella pendula is indigenous to both areas with 2 additional species in Japan and 2, in Mexico.

Homaliadelphus sharpii is found in both countries with 2 other species in Japan.

Haplohymenium triste is common to the two regions with 3 additional species in Japan.

Anomodon is represented in Mexico by 4 species two of which (*A. minor* and *A. viticulosus*) are among the 8 present in Japan.

Herpetineuron toccoae is the only species in the genus indigenous to Japan and to Mexico.

Haplocladium microphyllum is reported from both countries but Japan has 8 other species.

Thuidium, better represented in Japan (about 35 species) than in Mexico (6), has only *T. delicatulum* common to both.

Campylium has 3 "common" species: *C. chrysophyllum*, *C. hispidulum*, and *C. stellatum*, with a total of 7 in Japan and 4 in Mexico.

Leptodictyum, with 5 species in Japan and 3 in Mexico, has only *L. riparium* common to both lists.

Hygroamblystegium has only *H. tenax* among the 4 species reported from Japan and the 2, from Mexico.

Amblystegium serpens represents the genus in both countries, which has 10 species in Japan and 3 in Mexico.

Drepanocladus has 9 species in Japan and 3 in Mexico, of which *D. exannulatus* and *D. uncinatus* are found in both regions.

Platyhypnidium riparioides is the only species in Japan, and it and 2 others are reported from Mexico.

Brachythecium salebrosum is the single species of the genus in both areas—Mexico has about 20 species and Japan 38.

Eurhynchium has 12 species in Japan, of which 2, *E. praelongum* and *E. pulchellum*, are the only species of the genus in Mexico.

Pterigynandrum filiforme is the only representative of the genus in Japan and in Mexico.

Plagiothecium denticulatum is the only Mexican representative of the genus; it is among the ± 15 species in Japan.

Heterophyllium affine (*H. nemorosum*) is the only Mexican species of the genus which is represented in Japan by it and 4 other species.

Hypnum, a relatively large genus in Japan (about 20 species) but with only 8 in Mexico, has only *H. cupressiforme* in both.

Rhytidium rugosum represents the genus in both areas.

Diphyscium foliosum is the only species common to Mexico and Japan—the latter has a total of 5 species.

Oligotrichum aligerum is found in Mexico and in Japan which has 2 additional species of the genus.

Polytrichum is represented by 3 species in Mexico: *P. commune*, *P. formosum*, and *P. juniperinum*, all of which are among the 10 reported from Japan.

Thus it appears there are 65 genera with about 93 species which have been reported from both Japan and Mexico. Of these species, several might be considered more or less cosmopolitan with little geographical significance, *e.g.*, *Ceratodon purpureus*, *Weissia controversa*, *Funaria hygrometrica*, *Bryum argenteum*. Others present ranges of unusual interest, *e.g.*, *Fissidens garberi*, *Aongstroemia orientalis*, *Brothera leana*, *Symblepharis helicophylla*, *Venturiella sinensis*, *Homaliadelphus*

sharpii, Heterophyllium affine, inter alia. Certain related, or vicariad, or perhaps conspecific taxa, *e.g., Hypnodontopsis apiculata* and *H. mexicana, Pogonatum spinulosum* and *P. pensilvanicum, Entodon angustifolius* and *E. macropodus,* and *Trachypodopsis crispatula* and *T. otiophylla* present ranges that are extremely interesting. The ranges of many taxa need to be studied further before their geographical significance can be determined. Moreover, additional monographic work may well increase the number of species common to both Japan and Mexico.

Of interest too, are certain species reported from Guatemala by Bartram (1949), which are common to Japan but unreported from Mexico (although most are present north of Mexico). These include *Trichostomum cyclindricum, Barbula reflexa, Orthotrichum anomalum, Hookeria acutifolia, Cratoneuron filicinum,* and *Hylocomium brevirostre.* They should be searched for in Mexico, but if they are absent, their disjunctive ranges would be particularly intriguing.

It is clear that the Japanese moss flora is richer than that of Mexico. If we ignore those common to both countries, Japan has about twice as many genera as does Mexico and well over twice as many species. In the genera common to both areas, the Japanese species far outnumber the Mexican. While further study, particularly monographic work, may reduce the number of taxa, the disparity between the moss floras of Japan and of Mexico will remain, even if somewhat diminished.

This disparity in the richness in the two floras may be due in part to the geological histories of the two regions, and in part to the present environments. According to Schuchert (1935) Mexico was relatively low (and probably tropical) almost until the Pliocene, and at present a large part of that country is too arid for the development of a bryophytic flora comparable to that of Japan. In contrast, the geological history of Japan and its present environments are such as to facilitate the development and retention of an extremely rich bryoflora.

Although this is only a preliminary statement, it does suggest that there are common to Japan and to Mexico certain species with disjunctive ranges which require studies and explanations.

Acknowledgments

This manuscript was prepared under the Japan-U.S. Cooperative Science Program with the aid of grant no. GF-149 from the National Science Foundation and Grant no. 23 from the Japan Society for the Promotion of Science.

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THE PROBABLE GROWTH HABIT OF THE EARLIEST FLOWERING PLANTS

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About a hundred years ago, Charles Darwin referred to the origin of the Angiosperms as an "abominable mystery." Modern research, although it has shed light on many of the problems which in Darwin's day were mysterious and unsolved, has done little to clarify this problem. It still occupies the thoughts of many botanists interested in evolution, to their bewilderment and frustration.

The reasons for this difficulty are manifold, but lie chiefly in the imperfection of the fossil record. Clear evidence regarding the origin and early evolutionary history of angiosperms would need to consist of a series of well preserved reproductive structures connecting the most primitive angiosperms with non-angiospermous seed plants, comparable to the fossil series which Florin (1951) has used so brilliantly to interpret the origin and evolution of the conifers. We do not have even the beginnings of such a series. Instead, we have only detached leaves, fragments of wood, and pollen grains. All of these kinds of fossils are clearly unreliable for tracing evolutionary phylogenies. Typical angiosperm leaves are simulated by the leaves of *Gnetum,* which most botanists, including the present writer, regard as a highly specialized side line, far from the ancestry of the angiosperms. On the other hand, some angiosperms, such as *Kingdonia* and *Circeaster* (Foster, 1959, 1963), have leaves with such an anomalous venation pattern that if they were found as fossils, unaccompanied by reproductive structures, they would not be recognized as angiosperms at all. The degree of specialization in wood structure, as Bailey (1944, 1953, 1957) has pointed out, is very poorly correlated with the degree of advancement in respect to reproductive parts. The wood of primitive, vesselless angiosperms is hard to distinguish from that of Pteridosperms and other non-angiospermous seed plants. In respect to pollen, identification is relatively easy and definite if one is dealing with close relatives of modern forms, but would be hopelessly uncertain if we were dealing with forms very different from any of those living today, which I believe must have been the nature of the common ancestors of monocotyledons and dicotyledons. Consequently, none of these frequently preserved parts, even if present in a complete sequence connecting angiosperms with their presumed ancestors, would by themselves provide evidence regarding angiosperm phylogeny, unless they were accompanied by macrofossils of reproductive parts.

Faced with this virtual absence of clearly recognizable fossils, many botanists have abandoned as hopeless any attempts to solve the problem of angiosperm origins. Such an attitude is in many ways justified. Nevertheless, this problem is of such importance for understanding the evolution of higher plants that many hypotheses and speculations about angiosperm origins have been and are still being

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put forward. Such speculations should be critically reviewed in the light of our increasing knowledge about the processes of evolution.

One such speculation, offered by Melville (1960), is that the earliest angiosperms may have looked so different from the conceptions about them which are held by most contemporary botanists that we would not recognize these forms as related to flowering plants even if we did find them as fossils. I shall not attempt in this article to review the revolutionary ideas about the nature of the angiosperm flower which form the basis of Melville's speculations. I shall, rather, review some current ideas another characteristic of primitive angiosperms, their habit of growth.

THE BASIS FOR THE BELIEF THAT ANGIOSPERMS WERE ORIGINALLY WOODY

Plant anatomists are now nearly unanimous in their belief that the original angiosperms were woody, and that the herbaceous growth habit is in all instances derived from an ancestral woody condition (Metcalfe & Chalk, 1950). The general acceptance of this hypothesis followed the publication and wide popularity of E. C. Jeffrey's (1916) "Anatomy of Woody Plants" and the nearly contemporary work of Eames (1911) as well as Bailey & Sinnott (1914). Jeffrey advanced the hypothesis that the herbaceous condition was derived from woodiness through an increase in the amount of ray parenchyma tissue surrounding the bases of the leaves. In this way, the originally continuous woody cyclinder became broken up into separate vascular bundles. This type of change probably accompanied the origin of many herbaceous forms, including the ancestors of the monocotyledons. Nevertheless, many herbs belonging to both primitive and relatively advanced families possess continuous vascular cylinders, containing rays no wider than are those of typical woody stems. Bailey & Sinnott, therefore, rejected Jeffrey's hypothesis as a general explanation for the origin of the herbaceous condition, and their verdict is now generally accepted (Metcalfe & Chalk, 1950).

Bailey & Sinnott gave the following reasons for believing that herbs are derived from woody forms:

1. Reduction in cambial activity, by means of which the amount of woody tissue in the stem becomes reduced relative to pith and cortical tissue, can be traced in many phylogenetic lines constructed through comparisons between modern forms, and is a part of the general tendency for reduction which exists throughout the higher plants.
2. All of the non-angiospermous seed plants (conifers, *Gnetales, Ginkgoales*, cycads) are basically woody, in that their stems possess a continuous vascular cylinder.
3. The earliest known fossil angiosperms all belong to woody families.
4. In floras which on the basis of their present geographic distribution appear to be ancient, woody forms predominate.

In my opinion, none of these arguments can be regarded as general and irrefutable, and even when all four are taken together, they by no means constitute proof that the trend from the woody to the herbaceous condition is always in one

direction. The possibility that some woody plants are secondarily derived from herbs should not be disregarded.

REVERSIBILITY OF TRENDS IN GROWTH HABIT

The validity of the first argument depends upon the degree to which one accepts the so-called "Principle of Irreversibility" in evolution, sometimes designated "Dollo's Law." This principle has been critically reviewed by Simpson (1953, pp. 310-312) largely on the basis of his wide knowledge of the fossil sequences in molluscs and particularly vertebrates, which include the most complete sequences known to us. He points out that reverse mutation for most, it not all, individual characteristics is a well known fact of genetics. Moreover, reversals of direction in respect to single characteristics are recorded in many fossil sequences. An example is body size in the evolution of horses.

Whatever validity exists for the principle of irreversibility is based upon the fact that evolutionary advances consist of parallel and integrated changes in a large number of characteristics controlled by different genes which are capable of segregating independently from each other. The integration of these gene complexes is produced by the action of natural selection, which builds up successions of adaptive gene complexes in response to progressively changing environments. If the direction of environmental change becomes reversed, the evolutionary line of organisms is much more likely to develop superficially similar but fundamentally different adaptations to such reversals than it is to retrace the complex path by which it originally evolved, and revert to an adaptive complex like those of its remote ancestors. When terrestrial vertebrates, such as reptiles or mammals, became readapted to aquatic life, they became fishlike in appearance; but whales are fundamentally no more like fishes than are elephants or lions. When they reentered the water, the Podostemaceae took on an alga-like appearance, but fundamentally they are vascular plants and no closer to algae than are roses or saxifrages.

Applied to the evolution of growth habit, the principle of irreversibility as presently understood can tell us the following. Many plants have evolved a complex system of woody tissues, such as those of the more advanced angiosperms, in which many kinds of cells are differently adapted by their shape, wall structure, pitting, and cytoplasmic contents to perform separate functions of conduction, support, and storage. The growth and functioning of the stem depends upon a proper balance and integration between these different kinds of cells. Hence, we cannot expect such plants to reverse the numerous, integrated trends of specialization which produced this condition, and to evolve backwards toward a more generalized wood structure such as that found in gymnosperms. On the other hand, there is no reason to doubt that the genes controlling the amount of cambial activity could mutate either toward an increase or a reduction of this activity. Consequently, increase of woodiness is as much to be expected, given an environment in which it has an adaptive advantage, as is reduction of cambial activity and evolution toward the herbaceous condition. Furthermore, increase of "woodiness" through the development of a new kind of tissue is exactly the means by which one would

expect an ancestral herbaceous stock to give rise secondarily to woody derivatives. The secondary cambium which occurs between the vascular bundles of arborescent *Liliales* such as *Dracaena*, the sclerenchymatous cortical tissue of bamboos, and probably the interxylary phloem of many woody forms in the *Centrospermae* are cases in point. Sinnott & Bailey, in fact, recognize that in the monocotyledons shrubby and arboreal forms are derived secondarily from herbs.

If, therefore, we are to assume that all modern herbs are recent derivatives from ancestral woody stocks, we must reply on evidence other than the so-called principle of irreversibility. The second argument, that vascular tissue of herbs is more specialized than that of woody plants, is true in large part but by no means universally. Some strictly woody families, such as the *Bombacaceae, Burseraceae,* and *Meliaceae,* have relatively specialized xylem and phloem, while herbs such as *Paeonia* (Kumazawa, 1935) and many groups of vesselless monocotyledons (Cheadle, 1953) have vascular tissues which are more primitive than are those of most woody angiosperms.

RATES OF EVOLUTIONARY SPECIALIZATION IN WOODY PLANTS AND HERBS

Since the correlation between the herbaceous condition and specialization of woody tissue is imperfect, we must ask ourselves whether it could be based at least in part upon some other cause than that of unidirectional phylogenetic trends. Is it possible that the herbaceous condition is in itself a condition which increases the adaptive value of specialized vascular tissues? There is some basis for such an hypothesis. Herbs, particularly those growing in temperate climates or in the more arid portions of tropical regions, are usually adapted to undergoing regular cycles of rapid growth under favorable conditions, slower growth when conditions become worse, and dormancy during the cold or dry season. Furthermore, they often possess underground storage organs which help them to survive during unfavorable periods. Hence, we might expect them to evolve more efficient mechanisms for translocation and storage of food materials than would conifers or evergreen woody angiosperms, which maintain a slower but more continuous activity of metabolism and growth throughout most of the year.

Consequently, evolution in the direction of specialized vascular tissues could progress more rapidly in a line which was evolving the herbaceous growth habit than in a related line which remained woody. This would mean that families which acquired the herbaceous growth habit at an early stage in the evolution of angiosperms would even at this early period of time have evolved more specialized vascular tissues than their contemporary woody relatives. This seems to be the best way of resolving an apparently paradoxical situation. Many groups of herbaceous angiosperms, such as genera of *Ranunculaceae, Berberidaceae, Saxifragaceae,* and some families of monocotyledons, have relatively primitive reproductive structures as well as patterns of geographic distribution which suggest that they are very old. At the same time, their anatomical structure and vascular tissues are highly specialized. In my opinion, these groups are as old or older than many families of

woody angiosperms. At an early stage in angiosperm evolution they evolved a high degree of vegetative specialization, which they have retained ever since then.

EVIDENCE FROM THE FOSSIL RECORD AND FROM GEOGRAPHICAL DISTRIBUTION

The third kind of evidence which has led people to believe that the earliest angiosperms were trees is that from the fossil record. The fossil leaves and pollen which occur in the strata of lower to middle Cretaceous age, the earliest unquestionable angiosperms, resemble modern forms which are trees. This is also true of much more recent fossils, even those of early Tertiary age. Does this mean that herbs did not exist when the earliest angiosperms appeared?

Such an assumption would make extremely difficult the interpretation of disjunct distribution patterns in many modern herbaceous genera. Bailey & Sinnott correctly maintained that woody forms predominate among those species which have modern patterns of geographic distribution indicating that they are very old. Nevertheless, there are many examples of herbaceous groups which have similar relictual distribution patterns. As pointed out many years ago by Fernald (1931), and reaffirmed by many other plant geographers including the present writer (Stebbins, 1940), the presence of vicarious species in eastern North America and eastern Asia, as well as in such remote regions as subtropical Africa and South America, can be explained only by assuming that the common ancestors of these species became widely dispersed not later than the beginning of the Tertiary Period. Many of these species are herbs belonging to such specialized families as *Compositae, Gramineae,* and *Orchidaceae,* which must have had a long period of evolution at the level of herbs or shrubs before the common ancestors of the vicarious species in question evolved. The occasional presence in fossil beds of Cretaceous age of fragmentary remains belonging to grass-like plants, or to plants resembling water lilies and other herbs is further evidence that herbaceous forms were already developed in the Cretaceous Period.

The absence or scarcity of herbaceous and shrubby forms in the older fossil record is, therefore, best ascribed to the imperfection of this record. There are two reasons why the record should be biased in favor of trees. In the first place, leaves and pollen of trees are much more abundant in any forest than are those of shrubs and herbs. Secondly, the most favorable sites for deposition of fossils are lowland areas—stream banks, lake shores, and coastal plains (Axelrod, 1952, 1961). Even in regions with a relatively dry climate, such sites are likely to be occupied by well developed forests. The upland areas and steep mountainsides which are most favorable for the growth of shrubs and herbs are by their very nature particularly unfavorable for the preservation of fossils.

One feature of the fossil record points definitely to the conclusion that the absence or scarcity of shrubs and herbs in it is due to its imperfection and the biased character of the sample preserved. On the basis of the principles of modern genetics the belief that any major groups of organisms arose through the occurrence and establishment of a single "macromutation" is now untenable (Grant,

1963; Mayr, 1963). If, therefore, the earliest angiosperms were trees, then their immediate ancestors must also have been arboreal. But, as Axelrod (1961) has pointed out, if these pre-angiospermous seed plants were large trees, then they should have been abundant in the widespread forests of the Jurassic Period. Consequently, they would have been preserved along with the remains of the conifers and other trees which are known as fossils of Jurassic age. If the evolutionary line of seed plants which finally gave rise to angiosperms consisted of a long series of progressively more specialized forest trees, it should be as well preserved in the fossil record as that of the conifers, and the presence of Darwin's "abominable mystery" is incomprehensible. On the other hand, if the non-angiospermous seed plants which were the immediate ancestors of the earliest angiosperms were small plants, and particularly if they were insect pollinated, so that they shed very little of their pollen into the air, then their virtual absence from the fossil record could be explained.

ECOLOGICAL CONSIDERATIONS

If we recognize natural selection as the principle guiding force of evolution, we have another reason for believing that the earliest angiosperms were relatively small, short lived plants rather than large trees. Angiosperms are distinguished from other plants chiefly by various features of their reproductive biology, such as the carpel, the double integument of the ovule, the reduced number of mitoses in the male gametophyte, the fusion of the polar nuclei in the female gametophyte, and double fertilization. Collectively, these new features must have evolved through coordinated changes in a large number of genes. Such coordination could have been achieved only through relatively strong pressures of natural selection.

Populations of long lived trees living in an equable climate would not be subject to strong selective pressures for greater efficiency of their reproductive system. Each individual tree can, during its life time, produce millions of seeds. In a stable forest, replacement occurs only when an old tree dies, permitting one or a few younger ones to occupy its place. Under such conditions, species can survive even though their reproductive systems are relatively inefficient, provided that they have sufficient vegetative vigor and are well adapted to their habitat. It is certainly no accident that all of the modern conifers, cycads, and other non-angiospermous seed plants are long lived and live in relatively stable habitats. They can compete well with angiosperms under conditions which place a greater premium upon a highly efficient vegetative system than upon reproductive efficiency, but they have not been able to give rise to short-lived derivatives, in which efficiency of the reproductive system is necessary for survival and evolutionary success.

If by some miracle of reincarnation a botanist could be given a glimpse of the of the entire plant world of the Mesozoic era, he would probably recognize the early angiosperms or their immediate ancestors as having the greatest degree of reproductive efficiency possessed by any plants existing at that time. Moreover, they must have been members of a variety of structured plant communities which occupied various habitats, just as different kinds of plants do today. Since the forces of mutation, genetic recombination, and natural selection must have been acting in ways

very similar to their action in modern times, we might expect that the plants with the greatest reproductive efficiency would have occupied habitats similar to those occupied by the most reproductively efficient plants of modern times. Consequently, we can obtain the best idea of the habitats which saw the first evolution of angiosperms by inquiring, what are the ecological sites which today support plants with the highest degree of reproductive efficiency? Since these primitive angiosperms were almost certainly woody, we can, perhaps, obtain the best impression of this habitat by directing our attention to the shrubby representatives of the most advanced families of dicotyledons, such as the *Labiatae* and *Compositae*.

There is no doubt that such plants are most abundant and highly developed in semi-arid hilly or mountainous regions, such as coastal California, the Mediterranean region, the Mexican plateau, parts of the Andes mountains in South America, and the coastal hills and mountains of South Africa. They are, moreover, predominantly low shrubs rather than trees. On the basis of this reasoning, we would expect to find that the initial evolution of the new level of reproductive efficiency which characterizes angiosperms took place in such semi-arid, hilly or mountainous pioneer habitats.

The argument which has been presented in this discussion up to the present point can be summarized as follows. Several lines of evidence indicate that herbaceous angiosperms evolved almost or quite as soon as the flowering plants appeared, and that they have existed throughout the evolutionary history of the class. Due to the more equable conditions which prevailed during the Cretaceous and the first half of the Tertiary Period, which resulted in a much more widespread distribution of forests, the proportion of herbs in the floras of those more ancient times was almost certainly lower than it is now. Many woody groups must have given rise to modern herbaceous types as recently as the middle portion of the Tertiary Period. Nevertheless, the virtual absence of herbs from the older fossil record of angiosperms is much better explained as an artefact of the record than as an indication of the actual situation. There are, moreover, good reasons for believing that the earliest angiosperms and their immediate ancestors could not have been large trees.

On the other hand, one irrefutable argument exists in favor of the hypothesis that the earliest angiosperms, as well as their immediate ancestors, had the anatomical structure of woody plants. This is the fact that, so far as we know them, all known non-angiospermous seed plants, both living and fossil, are basically woody.

The logical reconciliation between these two lines of evidence, which appear at first sight to point in different directions, is the hypothesis which will be developed in the remainder of this article. This is that the earliest angiosperms, as well as their immediate ancestors, were low shrubs or subshrubs which occupied semi-arid pioneer habitats such as mountainsides and talus slopes. They might be visualized as similar in growth form to many species of *Polygonum, Eriogonum, Thymus,* and various genera of *Ericales* and *Compositae.* From such plants, evolution in the form of adaptive radiation gave rise in one direction to taller shrubs and trees, and in the other direction to various kinds of herbs, including monocotyledons. Evidence in support of this hypothesis will be presented from three major groups of

dicotyledons. They have been chosen from numerous possibilities because of their diversity, and because they include some of the most widespread trees of moist tropical forests.

SOME RELATIONSHIPS OF INDIVIDUAL FAMILIES

The first example is the order "*Gruinales*" of Wettstein, including *Rutaceae, Simarubaceae, Burseraceae, Meliaceae,* and *Sapindaceae.* Heimsch (1942) pointed out the cohesiveness of this group based upon their close resemblances in woody anatomy. In respect to floral structure, the most generalized family of this group is unquestionably the *Rutaceae* (Engler, 1931). In many genera of this family the flowers are completely regular, with all parts present and free from each other. In some genera the carpels are only partly united and at maturity form dehiscent follicles. In these groups, the embryo in the mature seed is surrounded by a copious endosperm. The groups in which these generalized floral characteristics are commonest are all in the subfamily *Rutoideae* and consist of the *Xanthoxyleae* subtr. *Choisyinae, Ruteae* subtr. *Rutinae,* and the tribe *Boroniae.*

In the *Rutaceae* as a whole, shrubby forms outnumber trees by about two to one, and the three groups mentioned above consist almost entirely of shrubs. The groups of *Rutaceae* containing the highest proportion of trees are in the subfamily *Flindersoideae,* in which the flowers have a trend of specialization toward zygomorphy; and the *Aurantoideae,* characterized by completely united carpels which form usually fleshly, indehiscent fruits. In both of these subfamilies, the mature seeds lack endosperm.

The family most nearly related to the *Rutaceae* is the *Simarubaceae.* Their flowers are in some ways more specialized than those of the generalized groups of *Rutaceae,* particularly in the reduction of the seeds per mature carpel to one, the prevalence of indehiscent, often winged fruits, and the reduction or disappearance of endosperm from the mature seeds. Their flowers are, moreover, much reduced in size, and are aggregated into compound inflorescences. In this family, the ratio of trees to shrubs is reversed as compared to the *Rutaceae;* trees outnumber shrubs about two to one.

In the *Burseraceae,* the floral specializations characteristic of the *Simarubaceae* occur to an even greater degree. The carpels are always completely united, the ovules are reduced to one or two per carpel, and the fruits are indehiscent. The flowers are small, in complex inflorescences, and the seeds lack endosperm. The pinnate or bipinnately compound leaves which characterize the family are probably also a specialization. The *Burseraceae* consist almost entirely of trees.

In the *Anacardiaceae, Meliaceae,* and *Sapindaceae,* trees outnumber shrubs by more than two to one. These families possess the same trends toward floral specialization as those of the *Simarubaceae* and *Burseraceae.* In addition, the *Meliaceae* have various strong specializations of their androecium, while the *Sapindaceae* tend to have zygomorphic flowers. In this group of families as a whole, therefore, the most generalized floral structure, in the *Rutaceae,* is associated with a predominance of the shrubby habit of growth, while the groups which are predominantly arboreal possess various specializations of their flowers, fruits, and seeds.

In the second group of families to be considered, those forming the order *Malvales,* the same trends are evident. The most generalized family of this order is the *Tiliaceae.* Within this family, the least specialized in floral characteristics are a group of six genera in the tribe *Tilieae* which have completely dehiscent fruits (Schumann, 1895). Two of these contain shrubs as well as trees, two are shrubs, one *(Corchorus)* contains shrubs and herbs, while the sixth, *Entelea,* is arboreal and monotypic. The genera of the *Tilieae* which have indehiscent fruits, including *Tilia* itself, are all trees. Of the other tribes, the *Apeibeae* consist of three genera, all of which contain shrubs. The *Brownlowieae,* which are strictly arboreal, are specialized in their calyx consisting of united sepals, their fruits, with ovules reduced to one or two per carpel, and their frequent reduction of endosperm. The tribe *Grewieae* is specialized in possessing an androgynophore, with filaments adnate to the bases of the carpels. In this tribe, nearly all of the arboreal genera have indehiscent friuts, which in some instances are winged, and some genera have, in addition, unisexual flowers.

Nearest to the *Tiliaceae* are the *Sterculiaceae.* The tribes of this family which have the most generalized flowers, with all parts present and separate, are the *Dombeyae* and *Hermannieae.* Of the eleven genera in these two tribes, seven are entirely shrubby, two contain both trees and shrubs, one is a tree, and one an herb. In the neighboring tribe *Buettnerieae,* all of the genera contain shrubs except for *Theobroma* and *Guazuma. Theobroma* is highly specialized in its cauliflory and indehiscent, pulpy fruits. The *Helictereae,* which are specialized in possessing an androgynophore, contain three strictly arboreal genera, and two which include both trees and shrubs. Finally the most specialized tribe of the family is the Sterculieae, in which the flowers are unisexual, apetalous, and possess a well developed androgynophore. This tribe consists entirely of trees.

The next family, the Malvaceae, consists almost entirely of shrubs and herbs. The most generalized flowers in this family are in the tribe *Hibisceae,* possessing capsular fruits. The genera of this tribe are predominantly shrubby, and many lines of evidence indicate that in this family herbs have been derived from shrubs. The final family of the order, the *Bombacaceae,* is in some ways the most interesting of all. Although very closely related to the *Malvaceae,* the *Bombacaceae* consist almost entirely of trees. Their capsular fruits and woody habit of growth, indicate a closer relationship with the tribe *Hibisceae.* According to Metcalfe & Chalk (1950), their wood is highly specialized, and in all features agrees closely with that of the *Hibisceae.* Another very interesting feature of the *Bombacaceae* is their series of chromosome numbers, which have now been counted in several genera (Baker, 1960, and unpubl.). All of them are high polyploids, apparently on a base of $x = 9$. The commonest somatic number is $2n = 72$. This basic number of $x = 9$ is found in most sections of *Hibiscus,* in which genus the number $2n = 72$ is also common (Menzel & Wilson, 1963). It seems likely, therefore, that the arboreal *Bombacaceae* have been derived from primitive shrubby members of the *Malvaceae,* tribe *Hibisceae,* or their immediate ancestors by a course of evolution which involved extensive polyploidy.

The third group to be considered, the family *Polygonaceae,* differs from the

others in being predominantly herbaceous and temperate in distribution. Although its relationships to other families are somewhat obscure, it certainly belongs to the order *Centrospermae,* which are predominantly temperate and herbaceous. The most generalized flowers of this family are in the genus *Polygonum.* Among these, the sections *Avicularia* and *Duravia,* both of which contain suffrutescent species, are probably the most generalized in habit of growth. Furthermore, personal observations on one species of this group, *Polygonum Bolanderi* Brew., indicate that it has a relatively primitive nodal anatomy. In this species, three leaf traces emerge from three gaps, while in most species of the family, including other species of *Polygonum,* five or more leaf traces are found.

From a primitive suffrutescent condition, genera and species in this family radiated along numerous lines of evolution to growth habits of various types: caulescent perennial and annuals, rhizomatous perennials, rosette perennials, and vines. Trees are found only in the subfamily *Coccoloboideae,* which is strictly tropical, and has the specialized characteristic of a furrowed endosperm, as well as the specializations of nodal anatomy which characterize most of the family. Three genera are predominantly or entirely arboreal: *Coccoloba, Ruprechtia,* and *Triplaris.* In its calyx of united sepals, which become fleshy at maturity to produce a berry-like fruit, *Coccoloba* is decidedly specialized. *Ruprechtia* and *Triplaris* are both dioecious, and in *Triplaris* the difference between staminate and pistillate flowers is very pronounced. These genera of tropical trees almost certainly are end points of lines of specialization which probably began with shrubs adapted to a warm, temperate climate.

GENERAL CONCLUSIONS REGARDING THE EVOLUTION OF GROWTH HABIT

The three examples selected here for detailed treatment are by no means the only ones which could have been chosen. Equally good cases could be made for the derivation of trees from shrubs in the *Dilleniaceae, Rosaceae, Leguminosae, Myrtaceae, Oleaceae, Ericales,* and many other groups.

A logical question which might be asked is: does this kind of evidence really indicate that trees have been derived from shrubs, or is it more likely that in each of the groups concerned there existed ancestral forms which were trees, but which had generalized floral characteristics similar to those now found chiefly in shrubs? Two reasons can be given for a negative answer to this question. In the first place, as pointed out earlier in this article, the selective pressures which might lead to modification or extinction would be expected to act less strongly on trees living in stable forest communities than on shrubs which are generally found in less permanent habitats. Hence, if the ancestors of these groups were trees, some of them should have survived as long as their shrubby relatives. Secondly, the kinds of specializations which are found in the various lines described above are those which are generally characteristic of trees, and which are developed to their highest degree in such trees of temperate climates as the *Fagaceae, Juglandaceae, Ulmaceae,* and *Betulaceae.* These are unisexual flowers, reduction in flower size, development

of complex inflorescences, reduction in number of seeds per carpel and of carpels per gynaecium, evolution of indehiscent fruits, and reduction in the amount of endosperm in the seed. In various combinations, these characteristics probably make up character complexes which have a particular high adaptive value in association with the arboreal habit of growth.

The fact must, of course, be recognized that trees are more common than shrubs in the most primitive angiosperms, the woody *Ranales*. These ancient types are, however, relicts of much larger groups, and the numerous forms which must once have connected the various isolated families of the group are now completely extinct (Bailey & Nast, 1945). In view of the probability that arboreal forms can, in general, outlast their shrubby relatives through a course of environmental changes over a long term period of evolution, the writer is inclined to believe that some, and perhaps most of the common ancestors of the contemporary families of woody Ranales were shrubs rather than trees.

The conclusions reached in this discussion should by no means be interpreted as meaning that the trend from shrubs to trees is an irreversible one. As stated at the beginning of the article, general trends such as those in growth habit might be expected to reverse themselves from time to time. Among modern, highly specialized woody families of temperate regions, such as the *Salicaceae, Betulaceae,* and *Fagaceae,* the reduction of growth habit from trees to shrubs and subshrubs has undoubtedly taken place many times. This has been in response to the exposure of members of these families to increasing drought and cold.

Lack of space prevents further exploration of the conclusions which have been reached. The relationships between dicotyledons and monocotyledons, the probable age of the angiosperms, and many similar questions deserve consideration and will be treated in future publications. The writer hopes that this brief new look at an old problem will stimulate other botanists to take a similar new look, and that some of them may likewise arrive at new conclusions.

SUMMARY

The hypothesis is advanced that the original angiosperms were woody shrubs or subshrubs, rather than trees as some authors have maintained. The trend from shrubs to trees is considered to be reversible, and evolution has progressed in either direction, depending upon the relationships between populations and their environment. The relatively high degree of specialization found in herbs is regarded as a result of stronger selection pressure for this condition rather than as evidence that herbs are necessarily more recent in their evolution than are woody plants. The geographic distribution patterns of many herbaceous groups of species suggest that they are very old. Their absence from the fossil record is, therefore, regarded as the effect of an expected bias in the record rather than as evidence that herbs did not exist during the earliest period of angiosperm evolution. Reasons are given for believing that the selective pressures which brought about the angiospermous reproductive condition would have acted more strongly on smaller, short lived plants inhabiting pioneer or relatively temporary habitats than on the trees of stable mesic

forests. Evidence that genera containing shrubs have less specialized reproductive characteristics than related, strictly arboreal genera is presented from three groups of angiosperms, the *Gruinales, Malvales,* and *Polygonaceae.*

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A NEW RECORD OF SCHNABELIA OLIGOPHYLLA H.-M. (VERBENACEAE) FROM SOUTHERN CHINA

By C. G. G. J. van Steenis
Rijksherbarium, Leyden

From the Edinburgh Herbarium I received an incertae sedis of herbaceous, completely aphyllous habit, but with remarkably 4-winged stems, bearing traces of small bracts below the decussate branchings. The flowers were beyond anthesis, two opposite on each constricted node; pedicels short but distinct, narrowly winged, bearing 2 minute bracteoles, thickened to the apex in a kind of ribbed hypanthium. No corolla or ovary could be found on our material, only a calyx of 4-5 narrow acute sepals, ca 5-6 mm long, standing out star-wise. The master set at Edinburgh had obviously a fruit or ovary, the notes on this reading: "Ovary 4 (or 2 dividing into 4); seeds apparently 2, attached basally."

The 4-angled stems, chorisepalous calyx, superior ovary, and (incomplete) description of the pistil led me to think of some sympetalous group, but the few ovules cq. seeds pointed to either *Labiatae* or *Verbenaceae.* Aphyllous plants are, however, rare in these families and those mentioned in the 1st edition of the Pflanzenfamilien did not fit. However, Dr. S. T. Blake, to whom I showed the plant, remembered an aphyllous Queensland Verbenacea, *Sparattothamnella juncea* (A. Cunn. ex G. Don) Briq. which indeed possesses also a star-shaped calyx in fruit and nearly winged stems. This stimulated attention towards *Verbenaceae.* In looking up the monograph of the Chinese *Verbenaceae* by Dr. Chien P'ei (1932) the only (monotypic) genus not known to me was *Schnabelia oligophylla* H.-M. of which the specific epithet sounded promising. But here the leaves were described as divided and only obsolete mention was made of the most prominent feature of our plant, viz. the remarkably winged stems.

A loan of the type from Vienna, by courtesy of Prof. Rechinger, proved, however, without a shade of doubt, that this was it. Obviously both the lower divided leaves and the upper reduced ones are fugacious or may occasionally be absent.

The localities of the sheets at hand are in three adjacent provinces of southern China, but scarcity of material may be due to rarity of the plant which was described very late.

Schnabelia oligophylla H.-M., Anz. Ak. Wiss. Wien **58** (1921) 92, fig.; Chien P'ei, Mem. Sc. Soc. China **1**, no. 3 (1932) 182 (Contr. Biol. Lab. Sc. Soc. China, bot. ser., **7**: 213); H.-M., Symb. Sin. **7** (1936) 909.

China: hunan: Lengschuidjiang, along Tsi-Diang R., above Hsinhwa, 200 m, on limestone, among shrubs, *Handel-Mazzetti 11967* (diar. 2475) (Vienna, holotype), fl rose with dark markings, 29-5-1918; also stream Lududsae (Laodao) between Hsinhwa and Wukang (H.-M. loc. cit.). kwangsi: N. Kwangsi, Lion Hill, 25 li N of Luchen, 300 m, tufted herb in deep ravine, very rare, *R. C. Ching 5428* (Vienna), fl purplish, 28-5-1928. kwei-

Ann. Missouri Bot. Gard. **52**(3): 469-471. 1965.

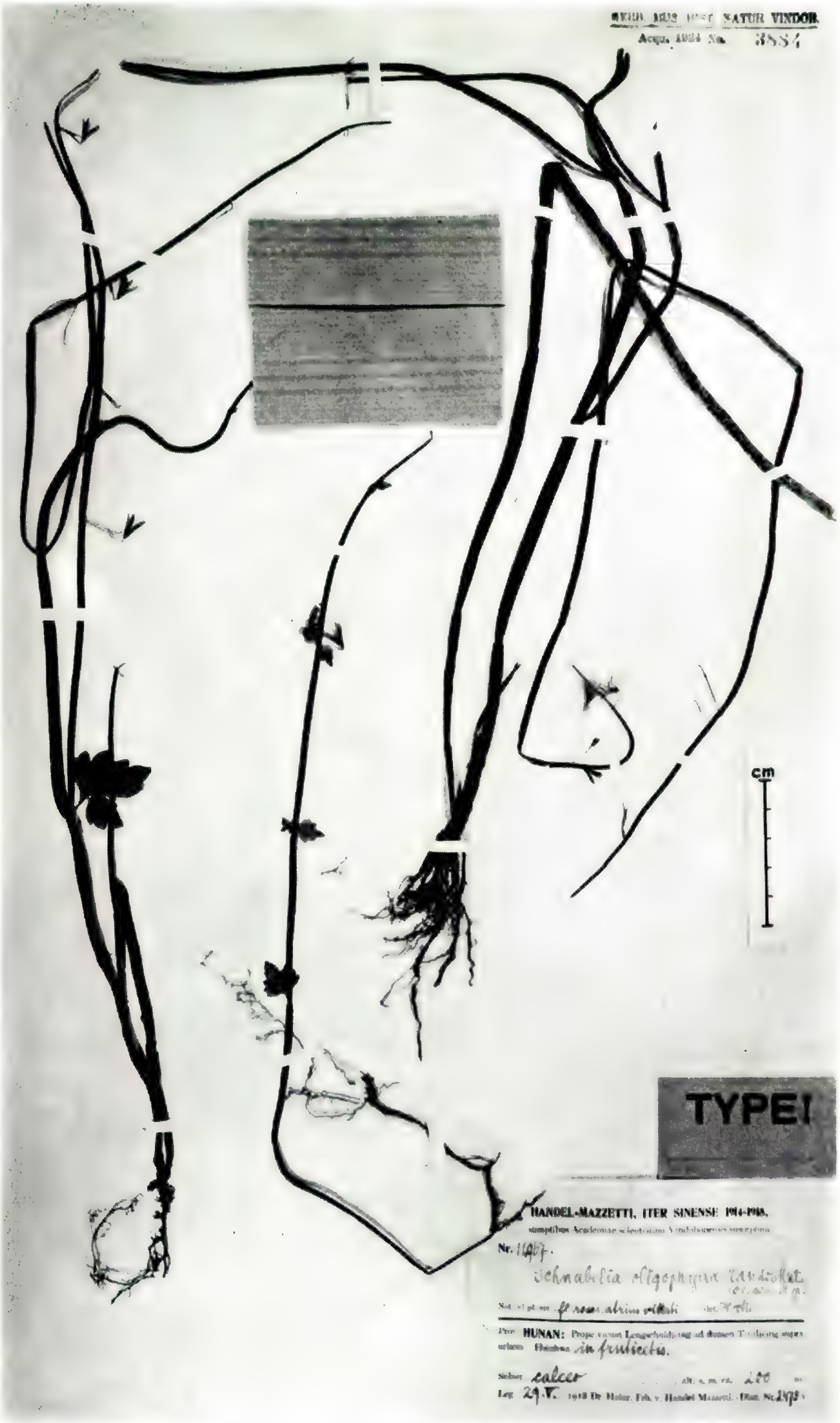

Fig. 1. Holotype of *Schnabelia oligophylla* H.-M.

CHOW: "grotte de sortie d'un petit ruisseau entre Kiang Long and . . . , *J. Esquirol 538* (Edinburgh) in herb. Léveillé, June 1905; "la nomme en chinois ku ku t'ay est là donné aux cochons. Pour moi je l'ai aperçu là seulement."

Chien P'ei, who did not see material, had some doubt about the disposition in the *Verbenaceae,* but the *Clerodendrum*-like corolla, bifid style, nerved calyx lobes, and paucity of seed agree well with this family.

Handel-Mazzetti (1936) assumed that *Ching 5428* might be a different species, but I believe only one species is concerned.

It would be very interesting to know whether or not *Schnabelia* has any true affinity with the Queensland *Sparattothamnella.* Obviously *Schnabelia* is a hygrophyte rather than a xerophyte.

THE GRASS GENUS LUZIOLA

By Jason R. Swallen
Key Biscayne, Miami, Florida

Luziola Juss. ex Gmel., Syst. Nat. ed. 13. **2**: 637. 1791.
Arrozia Schrad. in Kunth, Enum. Pl. **1**: 11. 1833.
Caryochloa Trin., Gram. Pan. 248. 1826.

Monoecious, the staminate and pistillate spikelets in the same or usually in separate inflorescences, the staminate usually terminal, the pistillate from the middle and upper nodes; glumes wanting; lemma and palea nearly equal, thin, several- to many-nerved, the nerves prominent in the pistillate spikelets; stamens several; stigmas long, plumose; caryopsis free, subspherical, smooth or minutely striate.

a. Pistillate inflorescence short, dense, glomerate, barely exserted from the lower sheaths.
  b. Branches of pistillate inflorescence conspicuously scabrous, not terminating in a spikelet; lemma and palea of pistillate spikelet easily disintegrating, leaving the scabrous nerves like awns surrounding the caryopsis .... 1. *L. spruceana*
  bb. Branches of pistillate inflorescence glabrous or nearly so, terminating in a spikelet; lemma and palea of pistillate spikelet not readily disintegrating ...... 2. *L. subintegra*
aa. Pistillate inflorescence expanded.
  c. Pistillate and staminate spikelets in the same inflorescence, partly enclosed in the sheath.
    d. Plants tufted; fruit 1.3-1.5 mm long, smooth or papillose; nerves of lemma and palea of pistillate spikelet very scabrous .... 3. *L. caespitosa*
    dd. Plants decumbent-spreading; fruit 2 mm long, smooth; nerves of lemma and palea of pistillate spikelet smooth. .... 4. *L. brasiliensis*
  cc. Pistillate and staminate spikelets in separate inflorescences.
    e. Fruit smooth or papillose, not at all striate. .... 5. *L. peruviana*
    ee. Fruit definitely striate.
      f. Pistillate inflorescence very inconspicuous, composed of two reflexed conjugate branches, each bearing 2-several short-pedicellate, appressed spikelets. Culms very slender, decumbent, forming dense tangled mats on water. .... 6. *L. fragilis*
      ff. Pistillate inflorescence composed of several to many plainly evident branches.
        g. Pistillate spikelets 1 mm long, the nerves of the lemma and palea densely scabrous .... 7. *L. gracillima*
        gg. Pistillate spikelets 1.5 mm or more long, the nerves entirely smooth.
          h. Pistillate spikelets ovate, the lemma and palea 2-3 times as long as the fruit. .... 8. *L. bahiensis*
          hh. Pistillate spikelets round or elliptic, the lemma and palea equalling the fruit or nearly so.
            i. Pistillate spikelets green, mostly short-pedicellate, 1.5-2 mm long.
              j. Pistillate spikelets 1.5 mm long, pyriforme. .... 9. *L. pittieri*
              jj. Pistillate spikelets mostly 2 mm. long. .... 10. *L. doelliana*
            ii. Pistillate spikelets purple, long-pedicellate, 2.5-3.5 mm long; panicles large, few-flowered. .... 11. *L. divergens*

1. Luziola spruceana Benth. ex Doell in Mart., Fl. Bras. **2**(2): 18. 1871.
Luziola spiriformis Anderss. ex Bal. & Poit, Bull. Soc. Hist. Nat. Toul. **12**: 232, *t. 5.* 1878.

Honduras: Lake Yojoa, *Edwards*. Brazil: amazonas: Paraná do Urariá, *Kuhlmann 1629*. pará: Maicurú, *Pires & Silva 4281;* Santarém, *Swallen 3303, 3305;* Boa Vista, Rio

Ann. Missouri Bot. Gard. **52**(3): 472-475. 1965.

Tapajos, *Swallen 3146, 3152, 3153, 3154.* PARAGUAY: Concepción, *Rojas 2671;* Central Paraguay, *Morong 556.*

2. LUZIOLA SUBINTEGRA Swallen, Ann. Missouri Bot. Gard. **30**: 165. 1943.

EL SALVADOR: San Vicente: Laguna Bruja, *Fassett 28390;* La Paz: El Rosario de La Paz, *Fassett 28318.* PANAMA: CANAL ZONE: Juan Mina, *Bartlett & Lasser 16816* (type); Rio Chagres, *Fairchild 2048.* CUBA: HABANA: Laguna de Ariguanabo, EKMAN *13436; Bro. León 4193.* HAITI: Massif du Nord, Guillotin, *Ekman H4802;* Massif de la Hatte, Etang-Miragoane, *Ekman H6471.* SANTO DOMINGO: SANTO DOMINGO: Rio Ozama, *Ekman 11589;* Haina, *Faris 266, 394.* TOBAGO: *Broadway 1626, 3100.* COLOMBIA: Cauca: Cienega de Agua Blanca below Cali, *Pittier 976.* BRITISH GUIANA: Georgetown, *Hitchcock 16537;* Blairmont, *Williams* in 1942; Demerara, *Harrison 1713;* 20 mi SE of New Amsterdam, *Little 16685; Jenman 1745, 4420, 4494.* SURINAM: Nickeie, *Semple 352;* Forest of Zandery, *Samuels;* Coronie, *Lanjouw 1127.* BRAZIL: MARANHAO: Monção, *Froes 20307;* PARÁ: Almeirim, *Ducke;* Cacaual Grande, *Camargo.* ECUADOR: Guayas: Guayaquil, *Asplund 5845.* PARAGUAY: Limpio, ROJAS *1664.*

3. LUZIOLA **CAESPITOSA** Swallen, sp. nov.

Culmi erecti 25-42 cm alti; vaginae aequantes 15-20 cm longae; ligula decurrens 7-8 mm longa; laminae usque ad 40 cm longae, 1-1.5 cm latae, glabrae; paniculae 10-18 cm longae, 4-6 cm latae, ramis solitariis usque ad 5 cm longis; spiculae stamineae 2.5-3 mm longae; spiculae femineae 1.3-1.5 mm longae, virides, nervatae; fructus papillosus, lucidus.

Perennial?; culms erect, 25-42 cm tall; sheaths equitant, compressed, keeled, glabrous, soft and more or less spongy, mostly 15-20 cm long; ligule decurrent, 7-8 mm long, thin; blades as much as 40 cm long, 1-1.5 cm wide at the widest part, gradually narrowed toward each end, glabrous on both surfaces, the margins very scabrous; panicle partly enclosed in the sheath or shortly exserted, 10-18 cm long, 4-6 cm wide, the branches solitary, ascending, the lower as much as 5 cm long; staminate spikelets 2.5-3 mm long, the lemma and palea thin, faintly nerved, glabrous, readily falling; pistillate spikelets 1.3-1.5 mm long, green, strongly nerved, the nerves scabrous; fruit shining, yellowish, papillose-roughened.

Type in the U. S. National Herbarium, No. 1257165, collected in shallow water below little falls, north of Cachoeira, Bahia, Brazil, 225 m alt, by *Agnes Chase* (No. *8102*). Also collected in Bahia, Brazil, by *Lutzelburg*, without locality (No. *2039*), at Cruz das Almas, by *G. Pinto* (No. *0312*), and Municipio de Serrinha, by *Eiten* & *Eiten* (No. *5013*).

4. LUZIOLA **BRASILIENSIS** (Trin.) Swallen, comb. nov.

Caryochloa brasiliensis Trin., Gram. Pan 248. 1826.
Arrozia micrantha Schrad. in Kunth, Enum. Pl. **1**: 11. 1833. Based on *Caryochloa brasiliensis* Trin.
Luziola micrantha (Schrad.) Benth., J. Linn. Soc. **19**: 55. 1881.

BRAZIL: Rio de Janeiro, *Kuhlmann 1916; Uhle 4971.*

5. LUZIOLA PERUVIANA Gmel., Syst. Nat. **2.** 637. 1791.

Luziola mexicana H. B. K., Nov. Gen. & Sp. **1**: 199. 1816.
Milium natans Spreng., Syst. **1**: 250. 1825.
Luziola brasiliana Moric, Pl. Nouv. Am. 94, *t. 60.* 1840.
Luziola leiocarpa Lindm., Kongl. So. Vet. Akad. Hand. **34**: 12, *pl. 8a.* 1900.

UNITED STATES: FLORIDA: Pensacola, *Curtiss 6871;* LOUISIANA: Plaquemines Parish, *Langlois 5, 45, 98;* New Orleans, *Silveus 4234.* MEXICO: Tlalnepantla, *Pringle 11227;*

Laguna del Negro, *Rovirosa 555.* Guatemala: jutiapa: Lago Retana, *Steyermark 32019; Huehuetenango*: Lago Ocubilá, *de Koninck 120;* jalapa: E of Jalapa, *Steyermark 32059;* alta verapaz: between Tactic and Tamahú, *Standley 90686;* San Cristobal, *Tuerckheim 8480;* Coban, *Tuerckheim 1209, 2454.* Peru: Lima, *Seeman 866; Ferreyra 2048; Anderson 584.* Brazil: rio grande do sul: Bagé, *Swallen 7450;* Pelotas, *Swallen 9136, 9148;* Uruaguaiana, *Swallen 7693;* Rio Grande, *Lindman A851;* São Leopoldo, *Orth 2517;* Vila Oliva, *Rambo 54926;* Caí, *Rambo 38802;* Farroupilha, *Rambo 40325;* Cacoeira, *Lindman A1213;* santa catarina: Massiambú, *Reitz & Klein 1323;* Ibirama, *Klein 2144;* Itajaí, *Smith & Klein 7286; Klein 1002;* Piloes, *Smith & Klein 7997;* Serra da Boa Vista, *Smith, Reitz & Klein 7963;* Mun. Lajes, *Smith & Klein 11348;* rio de janeiro: Serra de Itatiaia, *Chase 8367.* Paraguay: n. paraguay: *Fiebrig 4940;* central paraguay: *Morong 195;* Lake Ypacaray, *Hassler 12473.* Argentina: corrientes: Laguna Rincón, *Schwartz 8537; Parodi 6357;* tafi: *Venturi 2649;* monteras: *Venturi 1429;* chaco: Margarita Belen, *Aguilar 518, 1021;* salta: Alvarado, *Parodi 13485;* misiones: Apostoles, *Parodi 6949;* tucumán: Vipos, *Lillo 7933.*

6. Luziola **fragilis** Swallen, sp. nov.

Culmi gracilissimi, decumbentes, implicati; ligula hyalina 2 mm longa; laminae 1-4.5 cm longae, 1-2 mm latae, supra scabrae; spiculae stamineae 4-5 mm longae; spiculae femineae 2 mm longae, brevipedicellatae, appressae in 2 racemis conjugatis reflexis dispositae.

Perennial?; culms very slender, branching, decumbent and becoming tangled together; lower sheaths much shorter than the internodes, bladeless, the ends of the culm rising above the water for about 5-10 cm, the internodes becoming shorter and the sheaths overlapping, pilose; ligule hyaline, about 2 mm long; blades 1-4.5 cm long, 1-2 mm wide, finely scabrous on the supper surface; staminate spikelets in a simple terminal raceme 1-1.5 cm long with 5 or 6 short-pedicellate appressed spikelets 4-5 mm long; pistillate inflorescence composed of 2 short reflexed racemes 5-10 mm long; pistillate spikelets 2 mm long, purple, short-pedicellate, appressed, 2-6 on each raceme; lemma and palea 1.5-2 mm long, several-nerved, glabrous; fruit about 1 mm long, dark brown, shining, striate.

Type in the U. S. National Herbarium, No. 1961009, collected in banhado, Aquidauana, Mato Grosso, Brazil, June 24, 1946, by *Jason R. Swallen* (No. 9538).

This species was very common in a banhado (swamp) where it formed dense mats on the surface of the water. It is very different from other species of *Luziola* in the inconspicuous inflorescences which are nearly hidden in the foliage. The pistillate inflorescences are very characteristic with the two reflexed racemes, rather than the typical panicle of *Luziola.* There is no difference, however, in the spikelets. It also superficially resembles *Hydrochloa,* but in that genus the pistillate spikelets are arranged on one simple raceme, almost entirely hidden in the sheath.

7. Luziola gracillima Prodoehl, Bot. Archiv. Mez **1:** 241. 1922.

Mexico: jalisco: Guadalajara, *Pringle 3867* (type collection); sonora: Hermosillo, *Wiggins & Rollins 118.* Paraguay: chaco: Loma Porá, *Rojas 2761.*

8. Luziola bahiensis (Steud.) Hitchc., Contr. U. S. Nat. Herb. **12:** 234. 1909.

Caryochloa bahiensis Steud., Syn. Pl. Glum. **1:** 5. 1854.
Luziola alabamensis Chapm., Fl. South. U. S. 584. 1860.
Luziola longivalvula Doell in Mart., Fl. Bras. **2**(2): 17. 1871.
Luziola striata Bal. & Poit., Bull. Soc. Hist. Nat. Toul. **12:** 231, *t. 4, f. 2.* 1878.
Luziola pusilla S. Moore, Trans. Linn. Soc. Bot. II. **4:** 507, *pl. 37, f. 1-8.* 1895.

Luziola contracta Hack., Osterr. Bot. Zeitschr. **52**: 8. 1902.
Luziola bahiensis var. alabamensis Prodoehl, Bot. Archiv. Mez **1**: 242. 1922.

UNITED STATES: ALABAMA: Conecuh Co.: Brooklyn, *J. F. Beaumont;* Mobile Co.: *Mohr;* Langdons Station, *Mohr.* HONDURAS: MORAZÁN: El Zamorano, *Standley 28913;* Quebrada de Santa Clara, *Standley 22286.* CUBA: ISLA DE PINOS: Nueva Gerona, *Ekman 12383;* San Pedro region, *Killip 43688;* Santa Fé, *Britton, Britton & Wilson 15190; Ekman 12267;* PINAR DEL RIO: between Remates and La Fé, *Ekman 11315; Wright 3813.* SANTO DOMINGO: LA VEGA: Jarabaroa, *Ekman H14132;* SANTO DOMINGO: Villa Altagraria, *Ekman 11207;* SAMANÁ: Sanchez, *Ekman 15939.* COLOMBIA: META: San Juan de Arama, *Idrobo 493.* VENEZUELA: BOLÍVAR: Gran Sabana, *Steyermark 59219; Tamayo 2892;* Salto de Pacairao, *Steyermark 60492.* PERU: LORETO: Iquitos, *Killip & Smith 27181.* BRAZIL: AMAZONAS: Rio Branco, *Kuhlmann 3364;* PARÁ: Moju River-Estate Conceição, *Goeldi 157;* Belém, *Pires & Black 205;* SAO PAULO: "Campos das Sete Lagoas," *Eiten & Eiten 1971;* BAHIA: *Salzmann,* type of *Caryochloa bahiensis* Steud.; MINAS GERAIS: *Widgren;* PARANÁ: Ponta Grossa, *Swallen 8787;* Guaratuba, *Hatschbach 4012;* Tijucas do Sul, *Hatschbach 4320;* SANTA CATARINA: Joaçaba: Campos dos Palmas, *Smith & Reitz 9186;* Lebon Regis, *Reitz & Klein 11917;* Fazenda da Laranja, Bom Jardim, S. Joaquim, *Reitz & Klein 7893;* RIO GRANDE DO SUL: Fazenda do Arroio Osorio, *Rambo 45142;* MATO GROSSO: Aquidauana, *Chase 11032;* GOIAS: *Glaziou.* PARAGUAY: *Balansa 181* (type collection of *L. striata* Bal. & Poit.), *2956.* ARGENTINA: Misiones: Posadas, *Ekman 681.*

9. LUZIOLA PITTIERI Luces, J. Washington Acad. Sci. **32**: 159, *f.* 3. 1942.

VENEZUELA: GUARICO: Dos Caminos, *Pittier 12530* (type collection); Sombrero, *Pittier 12475;* Parmana, *Tamayo 4088;* BARINAS: Barinas, *Aristeguieta 2381.*

10. LUZIOLA DOELLIANA Prodoehl, Bot. Archiv. Mez **1**: 240. 1922.

BRAZIL: PIAUI: Fazenda Nacional to Picos, *Swallen 4215;* Picos, *Swallen 4222;* CEARÁ: Iguatú, *Swallen 4407;* Cratheús, *Swallen 4498;* Sobral, *Avelino & Black 115c;* PERNAMBUCO: Antennor Navarro, *Pickel 3810.*

11. LUZIOLA **DIVERGENS** Swallen, sp. nov.

Culmi erecti ca 35 cm alti glabri; ligula decurrens hyalina 5 mm longa; laminae 15-25 cm longae, 2-3 mm latae, marginibus scabrae; paniculae stamineae terminales, 7-9 cm longae, spiculis 5 mm longis; paniculae femineae 10 cm longae ramis paucis divergentibus, paucispiculis, spiculis femineis 2.5 mm longis, purpureis.

Perennial; culms erect, about 35 cm tall, glabrous; sheaths elongate, much longer than the internodes, glabrous; ligule decurrent, hyaline, about 5 mm long; blades 15-25 cm long, 2-3 mm wide, the margins very scabrous, the upper surface scabrous but less so; staminate panicles terminal, 7-9 cm long, the spikelets 5 mm long; pistillate panicles from the lower sheaths, about 10 cm long, nearly as wide with a few widely spreading to reflexed, few-flowered branches; pistillate spikelets 2.5 mm long, spreading, long-pedicellate, the lemma and palea purple, many-nerved, the nerves smooth; caryopsis dark brown at maturity, about 2.2 mm long, definitely striate.

Type in the U. S. National Herbarium, No. 1982914, collected in lake, Santa Terezinha, Ituiutaba, Minas Gerais, Brazil, February 18, 1950, by *A. Macedo* (No. *2165*). Also collected in the same locality by *A. Macedo* (No. *1658*), but the plants differ in having pistillate spikelets 3.5 mm long. No other differences are apparent, the whole plant having the same appearance as No. *2165.* The spikelets may be diseased.

SUGGESTIONS FOR THE APPLICATION OF EXPERIMENTAL TAXONOMIC TECHNIQUES TO SPECIES INDIGENOUS TO RHODESIA AND NEIGHBOURING TERRITORIES IN AFRICA

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Abstract

With the publication of the Flora Zambesiaca, progress in the orthodox taxonomic treatment of species from Rhodesia and neighbouring territories of South Central Africa has reached the stage where a number of problem species have been brought to light which should provide suitable material for more advanced methods of taxonomic research. A number of such species are listed with short notes on each for the benefit of future investigators in this field.

Introduction

The Flora Zambesiaca (Exell *et al.*, 1960-   ), which deals with the flora of Rhodesia, Malawi, Zambia, Mozambique and Bechuanaland Protectorate, has recently published the first part of its second volume (1963) and has Vol. 2, part 2, in the press. As each volume contains or will contain more than 600 species, it can be said that something in excess of 1200 species or more than 10% of the flowering plants have been dealt with in a reasonably careful orthodox taxonomic manner. In this process some groups have proved more difficult than anticipated and perhaps in some few cases a little easier. However that may be, it seems probable that the various authors of the different families have discovered and consequently revealed in their respective treatments those taxa which are genuinely difficult of definition or segregation by orthodox methods, using in the main characters of more or less superficial morphology.

Although experimental taxonomic research methods, using the most modern techniques of cytology, genetics, palynology, phytochemistry, and numerical plant taxonomy, have so far been more or less confined to European, N. American and some Asiatic taxa, it is felt that the time has been reached, through the publication of various regional floras in Africa, when a beginning could be made in a more advanced treatment of a number of Africa taxa. Furthermore, the growth of new African universities should mean that a proportion of such studies could be carried out in Africa itself. In the following few pages are suggestions based on the experience of the present author, partly in his preparation of various families for the Flora Zambesiaca, partly on treatments carried out by other contributors and partly on twenty years field experience in Rhodesia and neighbouring territories.

The writer is very grateful for the opportunity of dedicating these few suggestions to the memory of his old friend Professor Robert E. Woodson, Jr., particu-

Ann. Missouri Bot. Gard. **52**(3): 476-484. 1965.

larly in view of the latter's own pioneering efforts, in the application of numerical plant taxonomy and studies in hybridity, in his classical study of the North American *Asclepias tuberosa* (1947). Professor Woodson's influence was also more directly concerned since he and the writer carried on for a number of years an unusual exchange system whereby the Government Herbarium, Salisbury, supplied duplicate herbarium material in exchange for microcopies of botanical literature not available in Salisbury. As the shortage of literature is one of the principal difficulties in carrying on taxonomic work in the newer and more isolated herbaria, this exchange played a considerable part in making it possible for work on the Flora Zambesiaca to be carried out in Salisbury as well as in the more metropolitan centres of the British Museum (Natural History), Kew, Coimbra and Lisbon.

A very few studies using more advanced techniques making use of South Central African taxa have already been attempted, among which may be mentioned Tomlinson's (1964) study of the microscopic anatomy of *Triceratella* which aims at the elucidation of the relationship of this genus with its congeners in the *Commelinaceae*. Phipps (1964), having worked out a generic classification of the *Arundinelleae*, is now engaged in cytotaxonomic and numerical investigation in this group, including an investigation of the many species occurring in this area, and recently Professor A. S. Boughey, until lately Professor of Botany in the University of Rhodesia and Nyasaland in Salisbury has begun numerical taxonomic investigations into the variability of leaf shape in *Terminalia sericea* Burch. and the related species with which it may hybridise, *T. trichopoda* Diels and *T. brachystemma* Welw. ex Hiern.

Suggested Species Requiring the Application of Experimental Taxonomic Methods

1. *Clematopsis scabiosifolia* (DC.) Hutch., Kew Bull. **1920:** 20(1920).—Exell, Léonard & Milne-Redh., Bull. Soc. Roy. Bot. Belg. **83:** 407 (1951).—Exell & Milne-Redh., Fl. Zamb. **1,** 1: 93(1960).

The difficulties in the treatment of this species are well-known as they have now been referred to in the relatively recent regional floras of Angola, the Congo and East Tropical Africa. Sufficient to say that subspecific taxa are involved which however intergrade and which are defined in the Flora Zambesiaca merely as "groups" in the absence of a firm opinion as to whether the subspecific taxa involved are subspecies, varieties or assemblages of plants incapable of reliable separation at any level. There are some suggestions of incomplete geographical segregation and some groups are certainly extremely divergent from other groups. The problem is complicated by the fact that this perennial often grows in areas subject to annual fires which can produce temporary variation in leaf shape according to how recent or fierce a fire may have been. In addition, it seems likely that several basic species may be involved which hybridise with one another. The necessity for the observation of the various forms under cultivation, breeding experiments and cytological investigations is strongly indicated.

2. *Maerua juncea* Pax in Engl., Bot. Jahrb. **14:** 302(1891).—Wild, Fl. Zamb. **1,** 1: 218(1960).

Subsp. *junca.*

Subsp. *crustata* (Wild) Wild, tom. cit. 219.

These two species differ somewhat in the shape of their petals but there is an overlap in this character; they can only be separated reliably in fruit since the fruit of subsp. *juncea* is smooth whilst that of subsp. *crustata* is very rough. The minor but clearcut difference between these two taxa may only be due to a difference in a single gene.

3. *Hybanthus enneaspermus* (L.) F. Muell., Fragm. **10:** 81(1876).—Robson, Fl. Zamb. **1,** 1: 254(1960).

Five varieties are considered by Robson to occur in the Flora Zambesiaca area. Three of these, var. *nyassensis* (Engl.) N. Robson, var. *serratus* Engl. and var. *caffer* (Sond.) N. Robson show fairly well defined geographical segregation and would probably be better considered as subspecies. Apart from being widespread in Africa, the species also occurs in Madagascar, Comoro Is., Socotra, Arabia, tropical Asia, Malaysia and Australia. Variable species with inter-continental distributions are obviously worthy of further study. Var. *enneaspermus* shows weedy characteristics in our area and may have been introduced. Such an introduction could obviously have hybridised with indigenous forms and have helped to produce a complicated taxonomic pattern. The cultivation of forms from Africa and elsewhere under comparable conditions and experimental hybridisation is undoubtedly desirable.

4. *Flacourtia indica* (Burm. f.) Merrill, Interpr. Rumph. Herb. Amboin. 377(1917). —Wild, Fl. Zamb. **1,** 1: 286(1960).

A widespread species in Africa and also through Asia to China. This species shows extreme variability in indumentum, leaf-shape and presence or absence of spines. It also varies in habit from a shrub of savanna woodland to a 12 metre tall tree with fierce branching thorns in riverine fringes. A numerical taxonomic approach to leaf-shape and leaf-size might solve this problem of whether one or more species or subspecific taxa are involved.

5. *Scolopia zeyheri* (Nees) Harv. in Harv. & Sond., Fl. Cap. **2:** 584(1862).—Wild, Fl. Zamb. **1,** 1: 276(1960); **1,** 2: 565(1961).

A polymorphic "species" consisting of what may be ecotypes, subspecies or species, which are distributed respectively in submontane evergreen forest, open woodland or coastal bushland. The taxonomic situation is comparable with that of *Flacourtia indica* and numerical taxonomic methods may be of use.

6. *Silene burchellii* Otth. in DC., Prodr. **1:** 374(1824).—Wild, Fl. Zamb. **1,** 2: 352(1961).

Var. *augustifolia* which occurs in the Flora Zambesiaca area and throughout tropical Africa and in Arabia is very variable in itself and very distinct at first sight

from var. *burchellii* which is confined to the South Western and Eastern Cape Province of S. Africa. Whether var. *augustifolia* is merely subspecifically distinct or should be treated as a distinct species is not clear and cytological and plant breeding investigations are desirable.

7. *Psorospermum febrifugum* Spach, Ann. Sci. Nat., Bot., Sér. 2, **5:** 163(1836).—Robson, Fl. Zamb. **1,** 2: 387(1961).

An extremely variable species with a wide distribution in tropical Africa. Some of the variations are mentioned by Robson (loc. cit.) but, in addition, there is an extreme glabrescent form recently collected (*Wild* 6555 (SRGH) from Rhodesia, Melsetter District, Haroni Gorge) which, it is very difficult to believe, after seeing it in the field, is conspecific with the very tomentose forms mentioned by Robson. Numerical taxonomy and cultivation of the various forms might help resolve the problem.

8. *Hibiscus schizopetalus* (Mast.) Hook. f. in Curt., Bot. Mag. *t. 6524* (1880).—Exell, Fl. Zamb. **1,** 2: 470(1961).

Although there is evidence referred to by Exell (loc. cit.) that this plant is indigenous (although widely cultivated in Africa) in East Africa its laciniate petals and general appearance strongly suggest that it is a cultivar of *H. rosa-sinensis* L., a native of tropical Asia, which is widely cultivated in Africa and elsewhere. Genetical experiments with *H. schizopetalus* might find the answer to this problem.

9. *Dombeya burgessiae* Gerr. ex Harv. in Harv. & Sond., Fl. Cap. **2:** 590(1862).—Wild, Fl. Zamb. **1,** 2: 522(1961).

In particular, the two forms mentioned by Wild (loc. cit.) corresponding with the type of *D. burgessiae* from Natal, Swaziland and southern Mozambique and with the type of *D. rosea* Bak. f. from the Transvaal northwards to Kenya ought to repay experimental investigation. A numerical taxonomic examination of bract-shape might be a useful starting point.

10. ?*Melhania acuminata* Mast. × *Melhania forbesii* Planch. ex Mast.—Wild, Fl. Zamb. **1,** 2: 533(1961).

A putative hybrid with styles 4-6 mm long (intermediate between *M. acuminata* 7-11 mm long and *M. forbesii* 1-3 mm long). There is evidence (Wild, loc. cit.) that this putative hybrid occurs where the distributions of the two parents overlap or meet. In addition, one group superficially resembles *M. forbesii* (? back-crosses with *M. forbesii*). Others superficially resemble *M. acuminata*. Breeding experiments would effectively test the validity of this hypothesis.

11. *Grewia subspathulata* N. E. Br., Kew Bull. **1909:** 96(1909).—Wild, Fl. Zamb. **1,** 2: 51(1961).

A species morphologically intermediate between *G. bicolor* Juss. and *G. monticola* Sond. with the appearance of hybrid origin. Both these latter species frequently occur together in Southern Africa. Furthermore, as long ago as 1898, Mrs. Lugard, the collector of the types of *G. cordata* N. E. Br. (= *G. monticola*),

G. kwebensis N. E. Br. (= *G. bicolor*), *G. grisea* N. E. Br. (= *G. bicolor*), remarked on the label accompanying the type of *G. cordata* that "every hybrid seemed to exist in the Kwebe Hills (Bechuanaland Protectorate) between this species and *G. bicolor*." More recent collecting, not only in Bechuanaland but through the greater part of the Flora Zambesiaca area, seems to confirm her view. Although these *Grewia* species are woody shrubs and take a few years to grow to maturity, breeding experiments should be attempted.

Also under *Grewia bicolor* (Wild, loc. cit.) and other *Grewia* species it has been noted that the petals usually possess a basal nectary. When this is so the nectary rests against a glabrous basal portion of the androgynophore. In some cases the basal nectaries are absent and when this is so the glabrous basal portion of the androgynophora is also absent. Although the possession or absence of nectaries is almost certainly of no taxonomic significance and is genetically controlled within a single species, it would be interesting to prove this experimentally.

Grewia bicolor may also hybridise with *G. mollis* Juss. (Wild, tom. cit. 50) and *G. micrantha* Boj. (Wild, tom. cit. 54).

12. *Triumfetta tomentosa* Boj. [Hort. Maurit. 43 (1837) nom. nud.] in Bouton, Douz., Rapp. Ann. Maur. 19(1842).—Wild, Fl. Zamb. **1**, 2: 72 (1961).

Distinguished from *T. pilosa* Roth by fruits with straight or slightly curved setae at the apex of the aculei instead of uncinate setae. This separation is not entirely satisfactory. Both *T. tomentosa* and *T. pilosa* occur as weeds in the Flora Zambesiaca area and elsewhere and *T. pilosa* in particular is very variable with four named varieties in our area. Hybridisation is therefore quite likely. Alternatively, these two species may not be distinct. Cytological investigations and breeding experiments are indicated.

13. *Sparrmannia ricinocarpa* (Eckl. & Zeyh.) Kuntze, Rev. Gen. Pl. **3,** 2: 26(1898). —Weimarck, Svensk. Bot. Tidskr. **27:** 400-413 (1933).—Wild, Fl. Zamb. **1,** 2: 78(1961).

This species was divided into a number of subspecies by Weimarck (loc. cit.) but it has been noted by Wild (loc. cit.) that Nyasaland material is similar morphologically to subsp. *ricinocarpa* supposed by Weimarck to be confined to S. Africa whilst the Rhodesian material fits subsp. *micrantha* (Burret) Weim. which occurs also in Uganda and East Africa. The situation therefore seems somewhat confused and perhaps we are not dealing with true subspecies. The problem would need re-examination by cytological and breeding experiments.

14. *Dichapetalum cymosum* (Hook.) Engl. in Engl. & Prantl, Nat. Pflanzenfam. **3,** 4: 349(1896).—A. R. Torre, Fl. Zamb. **2,** 1: 324.

This plant is a common cause of cattle poisoning on the Kalahari Sands of Rhodesia, Bechuanaland Protectorate, S. W. Africa, the Northern Cape Province and the Transvaal. At one time the poisonous principle was thought to be a cyanogenetic glucocide but it has now been proved to be fluoracetic acid (for a comprehensive review of the toxic action of the plant see Watt and Breyer-

Brandwijk (1962) pp. 375-383). *Dichapetalum cymosum* was the first recorded plant showing this type of toxicity but it has now been shown that other *Dichapetalum* species (Watt & Breyer-Brandwijk, 1962, p. 383), i.e. *D. macrocarpum* Engl., *D. mossambicense* Engl., *D. stuhlmannii* Engl. and *D. venenatum* Engl. & Gilg contain the same principle. A chemotaxonomic investigation of the distribution of fluoracetic acid in other *Dichapetalum* spp. and in the various genera of the *Dichapetalaceae* might be profitable.

15. *Brachystegia* spp.

Although unfortunately cultivation of members of the genus requires a considerable number of years the genus should nevertheless offer a very fertile field to the experimental taxonomist. Wild (1951) has already shown that there is some correlation between rainfall in Rhodesia and the distribution of ecotypes of *Brachystegia spiciformis*. The correlation shows some weaknesses, however, and probably the picture is somewhat more complicated. Part of this complication is due to the fact that *B. spiciformis* hybridises freely with *B. glaucescens* Burtt Davy & Hutch. (? = *B. tamarindoides* Welw. ex Benth.) and produces fertile hybrids sometimes difficult to recognize for what they are in the herbarium although they are easily recognized in the field. In turn, there is a "low-altitude ecotype" of *B. glaucescens* occurring in the southeast of Rhodesia and Mozambique (Wild, 1955) which might repay experimental taxonomic examination. Mr. A. C. Hoyle of the Commonwealth Forestry Herbarium, Oxford, who has worked for many years on *Brachystegia,* is still in some doubt (personal communication) as to whether this taxon may not be a new species, but the position is bound to remain somewhat obscure in the light of orthodox taxonomic methods. Finally, *Brachystegia allenii* Hutch. & B. Davy hybridises freely with *B. boehmii* Taub. on the Zambesi escarpment in both Rhodesia and Zambia. Fertile hybrids forming a complete series between the parents are common and in places indeed seem to be more common than the parent forms.

16. *Ampelocissus obtusata* (Welw. ex Bak.) Planch., La Vigne Amér. **9:** 48(1885). —Wild & Drummond, Kirkia **3:** 16(1963).

This species, widespread between the Congo and Tanganyika in the north and the Transvaal in the south, includes two subspecies, *obtusata* and *kirkiana* (Planch.) Wild & Drummond, loc. cit. The range of the two subspecies overlaps somewhat and there are a few intermediates. *Ampelocissus pulchra* Gilg represents a form of subsp. *kirkiana* with dense capitate inflorescences. At present the species seems to be best treated as described above but the position is by no means clear and an experimental taxonomic approach seems desirable.

17. *Rhoicissus tridentata* (L. f.) Wild & Drummond, Kirkia **3:** 19(1963).

This species occurs in the Cape Province, Natal and the Transvaal, as well as throughout tropical Africa and in the Yemen. The species occurs in innumerable forms that at present defy analysis.

18. *Cyphostemma humile* (N. E. Br.) Descoings subsp. *dolichopus* (C. A. Sm.) Wild & Drummond, Kirkia **3:** 70(1963).

This subspecies occurs in Natal, the Transvaal and Rhodesia. In Rhodesia it is restricted to the serpentine soils of the Great Dyke, a remarkable geological phenomenon containing the largest deposit of metallurgical grade chrome ore in the world and forming an elongated mass of ultramafic and mafic rocks some 332 miles long and 3-5 miles wide (Wild, 1965). In addition to this subspecies there are numbers of other taxa, some newly described in the paper mentioned above which are either endemic to or, like *Cyphostemma humile* subsp. *dolichopus*, confined to the Great Dyke in Rhodesia but which occur in regions isolated from the Dyke either in Rhodesia or in other territories on soils other than serpentinised soils. This pattern of distribution agrees with the work of Stebbins (1942) who in dealing with this situation in the United States comments that the adaption to serpentine can be followed by biotype depletion and the development of some isolated populations into "insular" endemics and that this provides a reasonable evolutionary explanation for serpentine endemics. This matter is more fully discussed in the paper already referred to but truly endemic Dyke species in which biotype depletion is presumably complete belong to the genera *Lotononis, Pearsonia, Sutera, Heeria, Barleria, Vernonia,* etc. There is also the possibility, of course, that some of the Great Dyke endemics may have developed "ab initio" as also suggested by Stebbins and it is probable that the cultivation of these species and breeding experiments could soon reveal whether they did in fact exhibit extreme biotype depletion.

19. *Helichrysum maestum* Wild, Kirkia **4:** 152(1964).

This new species described in an article on the endemic species of the Chimanimani Mts. of Rhodesia is one of a series which the author (Wild, 1964) considers to be composed of vicarious pairs in the sense used by Cain (1944), i.e. "Vicarious species are closely related allopatric species which have descended from a common ancestral population and attained at least spatial isolation." In the case of the vicariads dealt with in this article one partner is endemic to the Chimanimani Mts. and the other in each case to some other mountain mass in neighbouring parts of Africa. A list of these suggested vicariads is as follows:

Aeschynomene aphylla Wild (Chimanimani)
    A. inyangensis Wild (Inyanga and Melsetter)
Hesperantha ballii Wild (Chimanimani)
    H. longicollis Bak. (S. Africa and Rhodesia)
Eriospermum phippsii Wild (Chimanimani)
    E. cecilii (Inyanga)
Helichrysum rhodellum Wild (Chimanimani, quartzites)
    H. acervatum S. Moore (Inyanga, Melsetter and Chimanimani Umkondo sandstones)
Plectranthus caudatus S. Moore (Chimanimani)
    P. crassus N. E. Br. (Mt. Mlanje)
Hemizygia oritrephes Wild (Chimanimani)
    H. obermeyerae Ashby (Soutpansberg)
Aloe munchii H. B. Christian (Chimanimani, quartzites)
    A. arborescens Mill., from the Cape to Nyasaland
Vellozia argentea Wild (Chimanimani, quartzites)
    V. velutina (Pax) Bak., Angola and the Zambezi Valley

Thesium chimanimaniense Brenan (Chimanimani, quartzites)
T. subaphyllum Engl., from Somaliland to Nyasaland
Thesium dolichomeres Brenan (Chimanimani, quartzites)
T. leucanthum Gilg, from Angola
Crotalaria phylicoides Wild (Chimanimani, quartzites)
C. caudata Welw. & Bak., from Angola
Rhynchosia stipata Meikle (Chimanimani, quartzites)
R. friesiorum Harms, from Kenya
Centella obtriangularis Cannon (Chimanimani, quartzites)
C. calliodus (Cham. & Schlecht.) Drude, from the Cape
Erica lanceolifera S. Moore (Chimanimani)
E. planifolia L., of the Cape Province
Erica pleiotricha S. Moore (Chimanimani, quartzites)
E. trichoclada Guthrie & Bolus, from Natal
Helichrysum maestum Wild (Chimanimani, quartzites)
H. pachyrhizum Harv., widely distributed through Southern Africa

A cytological study could presumably reveal whether these pairs should be considered as genuine vicariads, each pair derived from a common ancestor.

20. *Aspilia helianthoides* (Schumach. & Thonn.) Oliv. & Hiern in Oliv., Fl. Trop. Afr. **3:** 381 (1877).—Adams, Webbia **12:** 244 (1956); in Hepper, Fl. W. Trop. ed. 2, **2:** 239 (1963).

Adams (Webbia **12:** 245) has already remarked on the similarity of *Aspilia helianthoides* subsp. *helianthoides* to the type of *Aspilia africana* (Pers.) Adams. Both these taxa are extremely variable and "it is unfortunate that the Thonning type of *A. helianthoides* cannot be squarely placed near the centre of morphological variation of either of these two species but lies near the shadowy line of differentiation between them, albeit we continue to agree with Adams and with him place this specimen on the *A. helianthoides* side of the boundary" (Wild, in press). The position is further complicated by the fact that although in West Africa *A. africana* has yellow florets and *A. helianthoides* white (or cream), violet or purplish florets, in the Congo, East Africa and Zambia it has yellow flowers. *A. africana* is a perennial, although whether it is invariably so is difficult to tell from herbarium material, and *A. helianthoides* is an annual. Both species occur as weeds and Baker very recently (1964) has commented that the evolution of the weedy habit can often be accompanied by great plasticity of form. In these two *Aspilia* species there is certainly great plasticity and a strong suggestion of hybridity in West Africa at least where both occur together. Polypoid forms are also likely and in short a cytological and genetical investigation is necessary to elucidate the situation more adequately.

21. *Gloriosa superba* L., Sp. Pl. **1:** 305 (1753), sens. lat.

This extremely variable species is widespread in Africa and Asia. In practice, as has been mentioned already by Dyer, Verdoorn & Cood (1962, p. 20), it is not possible to separate it satisfactorily from *G. virescens* Lindl. *G. carsonii* Bak. and *G. rothschildiana* O'Brien may be little more than colour variants. On the other hand Mr. S. Percy-Lancaster, formerly of Salisbury, Rhodesia, but now of the Lucknow Botanic Garden, has brought into cultivation a large number of forms collected in the wild in Rhodesia. These were originally cultivated in Salisbury but

a proportion have now been taken to India. With the large number of forms available for examination in one place the differences are sometimes startling. Apart from the colour forms of yellow, yellow and red, plum colour, and forms with plane-margined (*G. virescens*) and undulate (*G. superba*) tepals, there are variants with and without leaf-apex tendrils, leaves alternate or opposite or ternate, erect forms and climbers. Variation is endless and one gets the impression that more than one species is certainly involved, complicated by endless hybrid forms which occur freely in the wild. Perhaps several species did once evolve in isolation but subsequent climatic changes allowed them to come together again before isolation was of sufficient length to allow genetic incompatibility to develop. Having remained inter-fertile endless hybridisation has now resulted. This should make a fascinating (and horticulturally rewarding) investigation.

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THE STORY OF TWO STERILE SPECIMENS

By Louis O. Williams
Chicago Natural History Museum, Chicago, Illinois

In 1943 the United States Forest Service sent a number of men to Costa Rica, assigned to give technical advice to the engineers building the Pan American Highway then being laid out and constructed. As an adjunct to the principal job, botanical material and wood specimens were collected from many timber trees along the route of the highway.

Dr. William A. Dayton wrote up the collection about ten years later (Phytologia **4:** 223-265. 1953) giving those determinations which Paul C. Standley, and others, had provided.

Two of these collections, *Barbour 1016* and *Dayton 3125,* were sterile but were named *Goethalsia meiantha* (Donn.-Sm.) Burret [*Tiliaceae*] by Standley.

Curiously enough H. A. Gleason received a flowering specimen of *Goethalsia* from Colombia (*Lawrance 494*) and came to the conclusion that the genus *Goethalsia* Pittier should have been referred to the *Flacourtiaceae.* He published an emended description (Phytologia **1:** 112. 1934) for the genus, placing it in *Flacourtiaceae.*

Professor Record studied the wood of two collections (Trop. Woods **40:** 18. 1934) and found that the wood suggested *Tiliaceae* and not *Flacourtiaceae.* The following year (Trop. Woods **42:** 21. 1935), Record received additional material and submitted it to Ducke and to Rehder for an opinion. Both thought it to be tiliaceous. In the same number of Tropical Woods, Standley reviewed Burret's "*Goethalsia* Pitt. doch eine Tiliacee, Keine Flacourtiacee" (Fedde. Rep. Sp. Nov. **35:** 195. 1934) in which Burret said that Gleason had misinterpreted the structure of the flower, that the plant was tiliaceous.

Charles Baehni wrote a short paper on the systematic position of *Goethalsia* (Candollea **6:** 44-45. 1935) concluding that it and three other genera normally included in the *Tiliaceae* should be transferred to the *Bixaceae.*

The next appearance in literature is that of Dayton mentioned in the second paragraph of this note, where *Dayton 3125* and *Barbour 1016* are indicated as "Gen. nov. (?)" but it is not quite clear in which family Dayton thought the "Gen. nov. (?)" belonged for he said below that "the leaf characters, including venation correspond with the botanical description of this species, [*Goethalsia meiantha*] and I am perfectly satisfied the material perfectly matches U. S. National Herbarium specimens thus labeled."

Under *Barbour 1016* just below Dayton quotes letters of both Record and Standley which indicate that the specimens belonged in the *Flacourtiaceae.*

Some years later Standley and I published *Hasseltia macroterantha* (Ceiba **3:** 53. 1952) based on collections made by Alexander F. Skutch. I had never seen and knew nothing of the history of the Dayton and Barbour collections and if

Ann. Missouri Bot. Gard. **52**(3): 485-486. 1965.

Standley recalled having previously worked with specimens like our proposed new species he did not add anything to our account that would reflect this.

In 1961, while revising the *Flacourtiaceae* for the Flora of Guatemala, I studied critically some of the entities in Central America and decided that *Hasseltia macroterantha* Standl. & L. Wms. was not a *Hasseltia* but that it represented an undescribed genus. The name *Macrohasseltia* [*Flacourtiaceae*] was proposed for it.

Dr. B. Francis Kukachka wrote in April 1964 to inquire if I had had occasion to examine some "controversial material" from Costa Rica while studying the *Flacourtiaceae* and mentioned *Barbour 1016* and *Dayton 3125.* He wrote that "the wood . . . . is definitely not *Goethalsia* and also neither *Hasseltia* nor *Hasseltiopsis* [= *Pleuranthodendron*] as has been suggested but is certainly a flacourt. . . . . To me the wood does not match any of the known genera but belongs in the group."

The "controversial material" was found in the herbarium still as *Goethalsia.* I recognized it as very similar to the recently described *Macrohasseltia,* which it proved to be upon critical examination.

Professor Pittier was a great believer in the usefulness of the *Flacourtiaceae* as a receptacle for all those things not recognized. "When in doubt put it in the *Flacourtiaceae*!" He must have had a strong feeling that his *Goethalsia* was tiliaceous, as in fact most now agree that it is.

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Volume LII 1965 No. 4

Annals
of the
Missouri Botanical Garden

November, 1965

PUBLISHED QUARTERLY BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN
AND WASHINGTON UNIVERSITY PRESS
ST. LOUIS, MISSOURI

Annals
of the
Missouri Botanical Garden

A quarterly journal containing scientific contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

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Information

THE ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Beginning with Volume 45, 1958:

Subscription Price	$15.00 per volume
Single Numbers	4.00 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Beginning June 1, 1962 the Stechert-Hafner Service Agency, Inc., 31 East 10th St., New York 3, N. Y., became sole agent for the ANNALS OF THE MISSOURI BOTANICAL GARDEN. The Agency handles all subscriptions, all claims beginning with volume 50 (1963) and all requests for back issues. Out-of-print numbers will be reprinted as may be required.

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Annals
of the
Missouri Botanical Garden

Vol. LII | November, 1965 | No. 4

FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 113. ELAEOCARPACEAE[1]

BY C. EARLE SMITH, JR.

Crops Research Division, Agricultural Research Service, U. S. D. A.,
Beltsville, Maryland

Trees or shrubs. *Leaves* alternate or opposite, simple, stipulate (at least in bud). *Inflorescences* generally axillary, rarely terminal, racemose, paniculate or reduced to a single flower. *Flowers* regular, perfect (rarely unisexual through abortion), 4- to 5-merous; sepals free or connate, valvate; petals free, rarely basally connate, sometimes incised or hairy, sometimes lacking; stamens numerous, usually free, borne on a fleshy receptacle, in the genus *Aristotelia* united into an androgynophore; anthers 2-celled, dehiscing longitudinally or by terminal pores, often surmounted by an awn; ovary superior, 2- to ∞-loculed (rarely 1-loculed), the ovules 2-∞ in each locule, anatropous, hanging; style entire or divided into as many lobes as there are locules in the ovary, or stigma sessile and sublobate. *Fruit* capsular, septicidally or loculicidally dehiscent, the locules ∞-seeded or, by abortion, 1-seeded, or fruit baccate or drupaceous; seeds naked or frequently arillate, the embryo straight, the endosperm copious.

Separated from the *Tiliaceae* primarily on the basis of the lack of mucilaginous ducts and canals.

This family of nine genera and 150 or more species is distributed throughout the tropical and subtropical areas of the world. Included are a few cold-tolerant species whose ranges extend into the warm-temperate zone. None are of more than

[1] Assisted by National Science Foundation Grant No. GB-170 (Principal Investigator, H. C. Cutler).

ANN. MISSOURI BOT. GARD. **52**(4): 487-495. 1965.

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. **52**, No. 3, pp. 223-486, was published on October 15, 1965.

local economic importance for lumber and only one or two species of *Aristotelia*, *Crinodendron* and *Elaeocarpus* have been planted as ornamentals. The Panamanian representatives of the *Elaeocarpaceae* are all forest trees of the genus *Sloanea* which occur only sporadically through the rainforest, except *Muntingia calabura* which may be shrubby.

a. Fruit capsular; flowers apetalous .... 1. SLOANEA
aa. Fruit baccate; flowers petaliferous .... 2. MUNTINGIA

1. SLOANEA[2]

SLOANEA L., Sp. Pl. 512. 1753.

Trees (rarely shrubs), the trunk often buttressed. *Leaves* alternate or opposite; stipules present, at least in bud; petioles various, often incrassate at one or both ends, terete or canaliculate; leaf-blades pinnately veined, the margin entire to dentate (spinose-dentate in 1 species). *Inflorescences* axillary, rarely terminal, commonly racemose or paniculate, occasionally corymbose, corymbo-racemose, or umbellate, ∞-flowered, rarely 1-flowered. *Flowers* with a calyx of 4 to 11 sepals, usually free; petals none (1 species with 2 whorls of perianth-parts of 4 members each); stamens ca 50 to more than 100, various, but always with the connective continued above the anther-sacs into a knob or awn; pistil 3- to 6-loculed, the ovules 8-10 in 2 rows per locule, with axial placentation; style entire or parted at the apex into as many branches as there are locules in the ovary. *Fruit* a loculicidally dehiscent capsule; valves 3-6, rigid, often woody; capsule unarmed, or armed with spines which may be firmly attached and flexible or rigid, straight or curved, or spines easily detached and irritant; seeds 1 or 2 per capsule (rarely 3) covered to the middle or almost completely covered by an aril growing from, and firmly attached to, the chalazal end (except 1 species without an aril), the raphe often prominent, the testa thin, the endosperm abundant, the embryo straight with thin, flat cotyledons.

Throughout tropical America from Nayarit, Mexico, and the Greater Antilles to northern Bolivia and southeastern coastal Brazil in Rio Grande do Sul.

None of the species of *Sloanea* are apt to be met with in casual, roadside collecting because they are predominantly trees of mature rainforest with a very scattered occurrence among the hundreds of species making up such an association. While the wood of many of the species is reported to be useful for timber and sometimes furnishes one of the preferred varieties of lumber in a local area, it cannot be profitably cut for export marketing because of its scattered occurrence. The aril around the seed is often reported to be edible, but both the quantity and the quality make it unlikely that *Sloanea* species will ever be exploited for their fruit.

[2] For complete generic and specific synonymy the reader may refer to C. E. Smith, Jr., The New World species of *Sloanea* (*Elaeocarpaceae*). Contr. Gray Herb. Harvard Univ. **175**: 114 p. 1954.

a. Sepals 4-11, unequal in size and shape, not covering the essential organs in bud.
  b. Sepals never more than 5.
    c. Pistil 2-4 mm long, ovary ovoid; capsule to 1.4 cm long, ellipsoidal; spines to 4.5 mm long, sparsely hirsute .... S. MEIANTHERA[3]
    cc. Pistil 5-7 mm long, ovary obovoid; capsule to 2 cm long, ovoid; spines to 1 cm long, glabrous .... S. PICAPICA[3]
  bb. Sepals 5-11, free, or the calyx a 4-6-lobed plate.
    d. Sepals free, 5-11; stamens separate.
      e. Flowers ca 4 mm in diam; capsule to 2.5 cm long; spines to 5 mm long, rigid .... S. FAGINEA[3]
      ee. Flowers generally 10 mm in diam or more.
        f. Stamens 10-11 mm long; anthers ovoid, pubescent; fruit subglobose with dense aculeate rufous setae (fide Pittier) .... 1. S. MEGAPHYLLA
        ff. Stamens 4-5 mm long; anthers elliptical, short-puberulent; capsule to 4.5 cm long, subglobose; spines to 3.5 cm long, puberulent .... 2. S. MEDUSULA
    dd. Calyx a 4-6-lobed plate; stamens forming a compact ball; capsule to 2.5 cm long, ellipsoidal; spines to 2.5 cm long, minutely puberulent .... 3. S. ZULIAENSIS
aa. Sepals 4, equal in size and shape, covering the essential organs in bud.
  g. Inflorescences umbellately 1-3-flowered; capsule to 2.5 cm long with clavate, irritant spines to 2 mm long .... 4. S. TERNIFLORA
  gg. Inflorescences corymbo-racemose, ∞-flowered; capsule to 3.5 cm long, unarmed, granulose, puberulent .... S. LAURIFOLIA[3]

1. SLOANEA MEGAPHYLLA Pittier, Repert. Sp. Nov. **13:** 312. 1914.

Tree to 25 m high, the trunk ca 40 cm in diam, with flat buttresses; branchlets robust; bark gray-brown, rough, somewhat striate. *Leaves* alternate; stipules to 7 mm long, obtuse, pubescent; petioles 9-11 cm long, robust, terete, striate, incrassate at both ends, glabrous; blades 34-62 cm wide, the shortest seen 58 cm long, elliptical-obovate, heavily rugose-coriaceous, the midrib, secondary and tertiary veins impressed, glabrous above, prominently puberulent to scattered-pubescent beneath, the secondary veins 12-18, arcuate-ascending, the base cordate, the apex obtuse, the margin irregularly undulate. *Inflorescences* 5-13 cm long, the peduncles, pedicels and bracts puberulent; peduncles 2.5-10.5 cm long, angled, striate; bracts 8-14 mm long, 0.5-2 mm wide at the base, lanceolate, sparsely dentate, obtuse. *Flowers* 1.0-1.5 cm long, 1.2-1.5 cm in diam; sepals 7-9, 7-9 mm long, 1-1.5 mm wide at the base, striate, densely puberulent without and within; stamens 10-11 mm long, the filaments 6-7 mm long, pubescent, the anthers 1-1.5 mm long, ovoid, pubescent, the connective prolonged into an awn 1.5-2.5 mm long, glabrous; pistil 14-16 mm long, the ovary to 3 mm long, 2.5-3 mm in diam, ovoid, 4-5-loculed, densely tawny-tomentose, the style 11-13 mm long, 4- or 5-angled at the base, 4-5-parted at the apex, pubescent $\frac{4}{5}$ of its length, glabrous on the apical $\frac{1}{5}$. *Capsule* not seen (Fruit subglobose with dense aculeate, rufous setae; capsule ca 2 cm thick, setae 4.5 cm long; seed 1 cm long; cf. Pittier, loc. cit. 312, 313).

[3]Species expected but not known to occur in Panama.

Although *S. megaphylla* was described many years ago from the Caribbean side of Panama, only one collection is known. It is a tree of the lowland rainforest and is perhaps restricted to riverine swamps as it was originally collected along the Río Fató. Along with other species of the association, this species is to be expected both east of Panama in Colombia and westward in Costa Rica and Nicaragua.

COLÓN: Río Fató, *Pittier 3920* (F, US).

2. SLOANEA MEDUSULA K. Schum. & Pittier, Repert. Sp. Nov. **13:** 312. 1914.

S. platyphylla Standley in Woodson & Schery, Ann. Missouri Bot. Gard. **27:** 318. 1940.

Tree to ca 40 m high or shrub; trunk with small plank buttresses; twigs slender to robust, more or less striate to angled-sulcate, puberulent to lanate-pubescent. *Leaves* alternate; stipules 1.5-3.5 cm long, 4-12 mm wide, elliptical-obovate, scarcely naviculate, the base rounded, the apex obtuse to acuminate-acute, the margin undulate to irregular, the adaxial surface glabrate to puberulent, the abaxial surface with glabrate to puberulent to densely pubescent midrib, the pubescence otherwide sparse; petioles 2-15 cm long, subterete, striate, glabrate to pubescent; blade 8.5-57 cm long, 3.5-31 cm wide, obovate to elliptical-obovate, chartaceous to coriaceous, the midrib and secondary veins subprominent, puberulent to pubescent above, prominent, glabrous to puberulent to pubescent beneath, the secondary veins 8-14, ascending, scarcely arcuate to arcuate, the base obtuse to rounded, the apex obtuse to acuminate-obtuse to acute. *Inflorescences* 4-18 cm long, the peduncles and pedicels puberulent to densely pubescent, the peduncles 3.5-15.5 cm long, often angled-striate, the pedicels 0.5-4 cm long, angled-striate, the bracts 0.5-1.5 cm long, 0.2-1.3 cm wide, lanceolate to obovate, subnaviculate, the apex acute to obtuse, the margin irregularly undulate to sparsely dentate, occasionally 3-lobed, pubescent overall, or, like the stipules, densely pubescent in the center, otherwide sparsely so. *Flowers* 0.7-1.8 cm long, 1-2 cm in diam; sepals 6-11, 3-10 mm long, 1-5 mm wide at the base, striate, deltoid to lanceolate, the apex obtuse to acute, occasionally bidentate, sparsely to densely pubescent without and within; stamens 4-6 mm long, the filaments 2-3 mm long, striate, enlarged upward to the anther-sacs, puberulent, the anthers 1-2 mm long, elliptical, short-puberulent, the connective prolonged into a short, sparsely puberulent awn; pistil 6-13 mm long, the ovary ca 2 mm long, 2-3 mm in diam, ovoid, 4- to 5-loculed, 4- to 5-rounded-angled, densely velutinous, the style 4-11 mm long, the basal ⅓ to ⅔ velutinous, the apex glabrous, scarcely or not parted, contorted or straight. *Capsule* reddish, to 4.5 cm long, subglobose (?), 4-valved, 1-seeded; valves to 7 mm thick, densely covered with rigid spines; spines to 3.5 cm long, tapering gradually to the apex, antrorsely puberulent; seeds ellipsoidal, almost covered by a reddish aril.

Sloanea medusula is primarily a tree of undisturbed forests where it is one of the dominants in the canopy. It occasionally persists as a clump of shrubby basal sprouts after clearing.

The species has been collected in rainforest from Guatemala through Central America to the Pacific coastal area of Colombia.

CHIRIQUÍ: Volcán Barú, *Stern & Chambers 65* (MO). COCLÉ: vic of El Valle, *Allen 1810* (type *S. platyphylla* F, MO, NY, US).

3. SLOANEA ZULIAENSIS Pittier, Bol. Com. Ind. Venezuela **4**(34): 31. 1923.—Fig. 1.

S. microcephala Standley, Field Mus. Pub. Bot. **4**: 152. 1929.

Tree to 27 m high; twigs moderately robust, striate, minutely fuscous-puberulent. *Leaves* alternate; stipules 12-20 mm long, 4-6 mm wide, lanceolate, naviculate, minutely puberulent, obtuse, undulate to repand-dentate; petioles 5.5-14.5 cm long, terete, striate, incrassate at both ends, subpuberulent to puberulent; blade 21-40 cm long, 8-23 cm wide, ovate to usually elliptical, chartaceous to subcoriaceous, the midrib and secondary veins distinct, puberulent above, the midrib on the underside under-cut next to the blade so as to appear almost terete, the midrib and secondary veins prominent, subpuberulent beneath, the secondary veins 12-15, arcuate-ascending, the base of the blade subacute to rounded, the apex obtuse to acuminate-obtuse or subacute, the margin irregularly undulate to repand-dentate to prominently obtuse-dentate. *Inflorescences* 13-27.5 cm long, the pedicels cymosely arranged at the ends of the branches of the racemes, the peduncles, pedicels and bracts minutely puberulent, the peduncles 12-26 cm long, striate, the pedicels 5-12 mm long, the bracts subtending the pedicels to 2 mm long, deltoid to lanceolate, obtuse, the bracts of the peduncle 3-10 mm long, ovate, naviculate, entire to sparsely dentate, obtuse, occasionally 3-lobed. *Flowers* yellow, fragrant, 2-3 mm long, 2.5-4 mm in diam; sepals united into a 4- to 6-lobed plate beneath the broad receptacle, or the margin of the calyx merely irregular, not lobed, puberulent within and without; stamens 1.5-2 mm long, the filaments to 0.5 mm long, angled, glabrate, the anther-sacs and connective spreading and truncate so that, at anthesis, the stamens form a subglobose mass with a mosaic-like surface; pistil to 3 mm long; ovary to 1.5 mm long, 1 mm in diam, ovoid, 4-angled, 4-loculed, finely and densely puberulent, the style to 1.5 mm long, tapered from the base, at times 4-angled, glabrous, the apex obtuse, entire. *Capsule* to 2.5 cm long, 2 cm in diam, ellipsoidal, 1- or 2-seeded, usually 4-valved; valves 2-4 mm thick, densely covered with reddish, semicurved, semiflexible spines; spines to 2.5 cm long, tapered from the base, scarcely minutely puberulent; seeds to 15 mm long, 7 mm in diam, ellipsoidal, almost completely covered with a 6-lobed aril, the 3 large lobes irregularly laciniate; aril firmly attached to the chalazal ⅓ of the seed.

Sloanea zuliaensis is the most distinctive species of the genus known in the American tropics. No other species has the stamens modified into a spherical, mosaic-surfaced mass from which the stigma protrudes. Like the other Panamanian species of *Sloanea, S. zuliaensis* is a canopy tree in rainforest.

The known geographical range of *S. zuliaensis* extends from the Pacific coastal forests of Costa Rica to the forests along the southwestern side of Lago Maracaibo in Venezuela.

CANAL ZONE: Barro Colorado Island, *Kenoyer 433* (type *S. microcephala* F, US). COLÓN: Río Sirri, *Pittier 4028* (US). DARIEN: vic of Caná, alt 2500 ft, *Stern et al. 526* (MO).

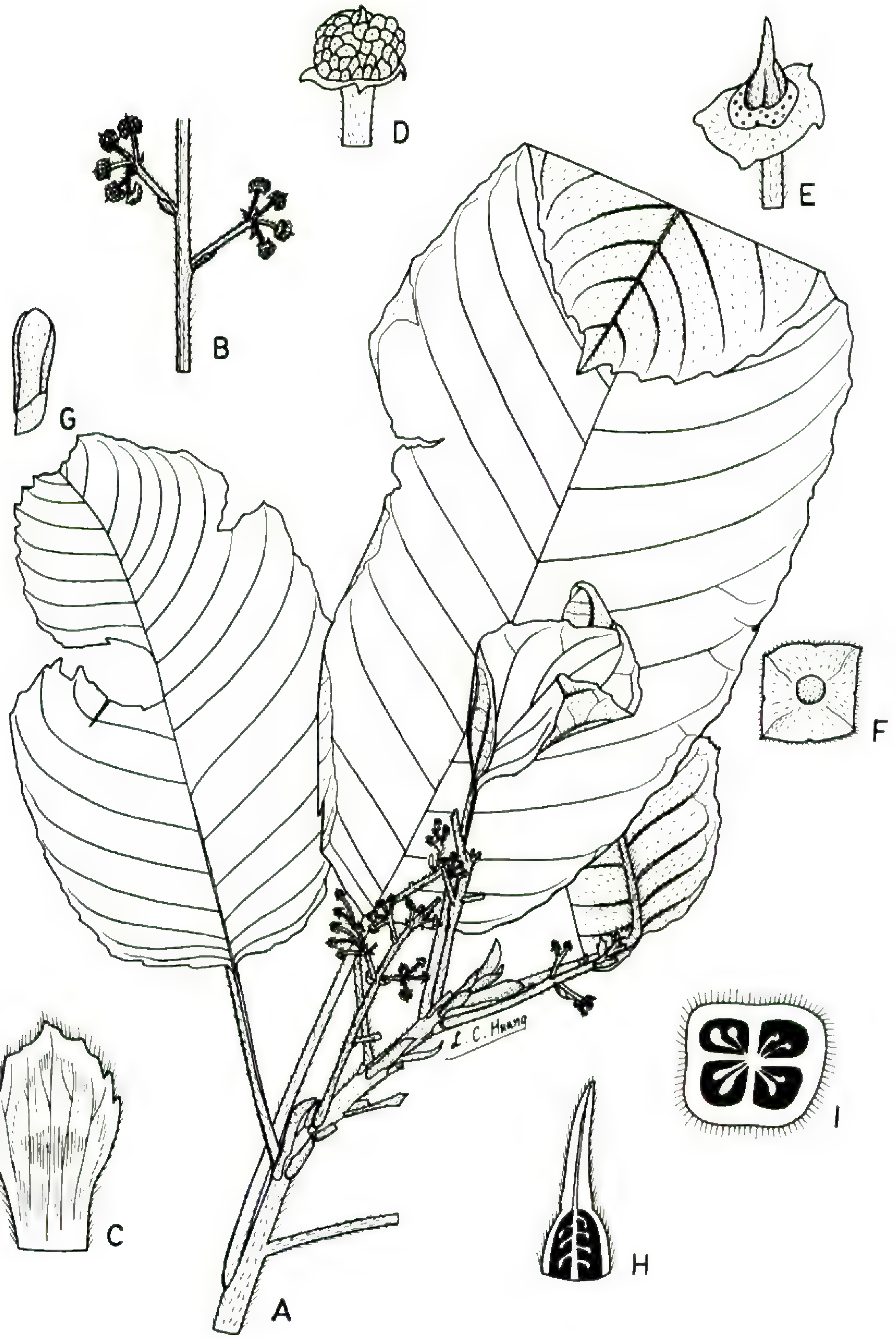

Fig. 1. Sloanea zuliaensis Pittier: A, habit (ca × 1/3); B, inflorences (ca × 1); C, bract (ca × 4.5); D, flower (ca × 3); E, id., anthers removed (ca × 5); F, calyx (ca × 5); G, stamen (ca × 8); H, pistil, longitudinal section (ca × 8); I, ovary, cross-section (ca × 15). After *Stern et al. 526.*

4. SLOANEA TERNIFLORA (Moc. & Sessé ex DC.) Standl., Trop. Woods **79:** 10. 1944.

Lecostemon terniflorum Moc. & Sessé ex DC., Prodr. **2:** 639. 1825.
Sloanea quadrivalvis Seem., Bot. Voy. Herald 85, *t. 15.* 1853.
Dasycarpus quadrivalvis (Seem.) Oersted, Vidensk. Medd. Naturhist. Foren. Kjobenh. 1855: 27. 1857.

Tree to 30 m high, the trunk buttressed, the bark smooth, black; twigs with brown or gray-brown, finely striate, often rugose bark, the new growth striate, minutely scattered-puberulent to puberulent. *Leaves* alternate to opposite; petioles 0.3-2 cm long, subterete, striate, minutely scatttered-puberulent to puberulent, often with a puberulent line on the upper side; blades 6.5-15 cm long, 3-7.5 cm wide, subovate to elliptical to obovate, firmly chartaceous to coriaceous, the midrib and secondary veins distinct to prominent, glabrous to puberulent above, glabrous to puberulent beneath, often light in color, the base subcordate to rounded to cuneate-obtuse, the apex rounded to obtuse to acuminate-obtuse, the margin entire to irregularly undulate to irregularly repand-dentate particularly toward the apex. *Inflorescences* 3.5-5.5 cm long, umbellately 1-3-flowered, the peduncles 1.5-3 cm long, striate, often laterally flattened, glabrous to finely puberulent, the pedicels 0.8-1.3 cm long, striate, glabrous to finely puberulent. *Flowers* maroon with pale yellow stamens, 5-7 mm long, 6-8 mm in diam; sepals 6-7 mm long, 2-5 mm wide, ovate, at times acuminate, minutely to finely scattered-puberulent without and within, the margins densely puberulent; stamens 3-4.5 mm long, the filaments 0.5-1 mm long, finely puberulent to puberulent, the anthers 1-2.5 mm long, elliptical to deltoid-lanceolate, finely puberulent to puberulent, opening by a lenticular pore at the apex, the connective prolonged into a finely puberulent to puberulent awn 0.5-1 mm long; pistil 4-5 mm long, the ovary 2-2.5 mm long, ca 1.5 mm in diam, ovoid, usually 4-loculed, puberulent to pubescent, the style 2-2.5 mm long, puberulent on the basal ⅓, glabrous above, the apex entire. *Capsule* 1.5-2.5 cm long, ellipsoidal, 1-2-seeded, 4-valved; valves 1-3 mm thick, densely covered with easily detached spines; spines ca 2 mm long, clavate, puberulent with antrorse flattened trichomes, the apex often with several longer trichomes; seeds 1-1.2 cm long, 0.5-0.6 cm in diam, ellipsoidal, almost entirely covered with an irregular-margined aril firmly attached to the chalazal ¼ of the seed.

Sloanea terniflora is found in the forests as one of the canopy trees and it also frequently persists in pastures and in second-growth following clearing of land. The capsules have a coarsely velvety appearance due to the closely-set but easily detached spines. The spines of the capsule can easily become embedded in the skin, hence the common name *terciopelo.*

Sloanea terniflora has been collected from Nayarit, Mexico, southward as far as Peru, Bolivia and Brazil.

CANAL ZONE: Chiva-Chiva trail, *Maxon & Harvey 6585* (GH, NY, US); Río Agua Salud nr Frijoles, *Piper 5863* (US); Albrook, *Dwyer & A. Robyns 175* (MO). CHIRIQUÍ: vic of David, *Pittier 2833* (US). COCLÉ: Río Mata Ahogada, *Allen 144* (A, F, GH). PANAMA: between Matías Hernández and Juan Díaz, *Standley 31959* (A, US); Juan Díaz, nr Panama City, *Pittier 2557* (F, GH, NY, US). VERAGUAS: *Seemann s.n.* (type *S. quadrivalvis* GH).

Sloanea meianthera J. D. Sm., Bot. Gaz. **37**: 208. 1904.

Although *S. meianthera* is unknown in Panama, the species is undoubtedly present as it is a widely ranging tree on the Atlantic slopes of mountains from British Honduras to eastern Costa Rica. It has never been collected at very high elevations. *S. meianthera* sometimes persists as a shrub or small tree on cut-over areas and in secondary forest.

Sloanea picapica Steyerm., Fieldiana: Bot. **28**: 360. 1952.

Species unknown to Panama although scattered collections have been made from Honduras to British Guiana primarily in the highlands. The wine-red capsules with sharp, rigid spines are very distinctive.

Sloanea faginea Standley, J. Wash. Acad. Sci. **15**: 478. 1925.

The species is known from several collections in Costa Rica. It should also be found in the forests on the slopes of Volcán Barú in Panama. Like other species of *Sloanea, S. faginea* is one of the canopy trees of the mature forest and would usually be unnoticed by the casual collector unless his attention were called to the tree by falling flowers or capsules.

Sloanea laurifolia (Benth.) Benth., J. Proc. Linn. Soc., Bot. **5**, Suppl. 2: 70. 1861.

The species is unknown in Panama although collections have been made in border areas of Costa Rica. *Sloanea laurifolia* is representative of the many species of the lowland rainforest which have a geographical range from Central America through northern South America into the Amazon basin. In his book, *The Rain Forests of Golfo Dulce* (1956), Allen notes on p. 325 that the wood of this species is supposed to burn when freshly cut even during rain, a singularly valuable attribute in this species' native habitat.

2. MUNTINGIA L.

Muntingia L., Sp. Pl. 509. 1753.

A monotypic genus widely distributed in tropical America.

1. Muntingia calabura L., Sp. Pl. 509. 1753.

Tree to ca 10 m tall or shrub; trunk usually slender, the bark black. *Leaves* alternate; stipules linear, 3-4 mm long, hirsute and glandular pubescent, usually soon caducous; petioles 2-5 mm long, densely hirsute and glandular; blades inequilateral, 5-11.5 cm long, 1.5-3.5 cm wide, lanceolate to elliptical, firmly membranaceous; midrib and secondary veins densely pubescent above, densely hirsute and glandular pubescent, prominent beneath; blade surface glandular, glabrate or with scattered stellate hairs above, densely matted-pubescent and glandular beneath; base strongly inequilateral, one side sometimes developing into an enlarged flap; apex acute to short attenuate, acute; margin serrate. *Inflorescences* supra-axillary, usually 1-flowered, infrequently 2-3-flowered; pedicels 1-1.8 cm long, hirsute and glandular-pubescent. *Flowers* ca 2 cm in diam; sepals 5, 5-7 mm long, 1.5-2 mm wide, lanceolate, long-acuminate, tawny-pubescent without, creamy-white, felty-pubescent within, caducous; petals 5, short-clawed, rhombic-ovate, creamy-white, 7-9 mm long, 5-8 mm wide, the outer margin undulate; stamens ∞ (more than 50), 4-5 mm long, borne on an enlarged hirsute receptacle; filaments slender; anthers ca 0.5 mm long, ovoid, reddish, the anther-sacs dehiscent their full length; pistil 4-5 mm long, nearly hidden by stamens and receptacular hairs; ovary ovoid, narrowing to a very short, thick style, smooth, glabrous, usually 5-loculed with bilobed placentae hanging free from near the top of the axis in each locule and covered on all surfaces with ovules; stigma thick, conical, 5-lobate.

Fruit baccate, yellow or dark red and sweet, in the specimens only to ca 8 (-10) mm in diam, surmounted by the persistent stigma, ca 5-loculed (locule walls apparently often displaced by the crowding of the mass of small seeds), the surface granulose; seeds ca 0.5 mm long, 0.33 mm in diam, ovoid, pale yellow.

Muntingia is widely distributed in tropical America in disturbed lowland areas. The fruit is edible, but it is too small and indifferent in flavor to have ever been considered for cultivation. The bark is reported to be stoutly fibrous and used in the manufacture of baskets.

CANAL ZONE: vic of Miraflores Locks, *Stern et al. 60* (MO); Paraiso Sta., Panama R. R., *Hayes 45* (MO); Cocoli Island, Miraflores Lake, *P. White 304* (MO). CHIRIQUÍ: vic of Puerto Armuelles, *Woodson & Schery 817* (MO). COLÓN: vic of Camp Piña, *Allen 3674* (MO). DARIEN: vic of Pinogana, *Allen 4289* (MO); Río Sabana, *King Léopold III 162* (MO).

While *M. calabura* is traditionally placed with the other genera in the *Elaeocarpaceae,* several characters of the plant point to this as a misalliance. Floral and fruit development and structure suggest affinities both with the *Tiliaceae* (from which the *Elaeocarpaceae* are barely separated) and the *Flacourtiaceae.* My examination of the herbarium material has been too cursory to suggest the true relationship of this species and I have had no opportunity to study the species in the field. Thus, reluctantly, I am including *Muntingia* with the *Eleocarpaceae.*

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 115. MALVACEAE[1]

BY ANDRÉ ROBYNS[2]

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Herbs, shrubs or small trees, mucilaginous, usually pubescent, ordinarily with stellate hairs, sometimes aculeate, infrequently lepidote. *Leaves* alternate, usually petiolate, stipulate, the stipules usually caducous, the blade simple or often palmately, seldom pinnately, lobed or parted. *Flowers* solitary or glomerate in the axils, or disposed in terminal, paniculiform, racemiform, spiciform, or corymbiform inflorescences, hermaphrodite, rarely imperfect, actinomorphous, usually 5-merous, with or without epicalyx; calyx valvate, usually lobed, dentate or truncate; petals hypoginous, contorted or imbricate, free or slightly connate together, adnate to the base of the staminal tube; stamens rarely 5, usually ∞, more or less long-monadelphous, the anthers 1-thecate or imperfectly 2-thecate, longitudinally dehiscent; pollen grains large, nearly always provided with spines; ovary superior, with usually 5-∞ carpels, the carpels 1- to ∞-ovulate, the placentation axile; style usually branched, the branches isomerous with or twice as many as the carpels, infrequently undivided and clavate; stigmas usually terminal and more or less capitate, sometimes decurrent on the style branches. *Fruit* a loculicidally dehiscent capsule or often a schizocarp separating into dehiscent or indehiscent mericarps, these arranged around a central columella, infrequently indehiscent and woody or fleshy; seeds 1-∞, commonly reniform or subglobose; endosperm usually scant or wanting; embryo generally curved; cotyledons foliaceous, often plicate.

A family of about 85 genera and 1500 species which is widely distributed in temperate and tropical regions, reaching high elevations only in the Andes. Cotton is the outstanding member of this family in economic value, and others furnish bast fibers that are used locally. The *Malvaceae* also include a few esculents such as okra, gumbo or marshmallow, but in general the family is poor in useful plants.

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[1] Assisted by National Science Foundation Grant No. GB-170 (Principal Investigator, H. C. Cutler).

[2] I wish to express my sincere thanks and appreciation to the directors and curators of the following herbaria for the facilities for study and/or for the loan of material: Chicago Natural History Museum (F), Gray Herbarium of Harvard University (GH), Royal Botanic Gardens, Kew (K), U. S. National Herbarium, Washington, D. C. (US), and School of Forestry, Yale University, New Haven (Y).

In the preparation of this treatment I made use of a manuscript by T. H. Kearney, which had been received at the Missouri Botanical Garden during or before 1952.

ANN. MISSOURI BOT. GARD. **52**(4): 497-578. 1965.

The flowers are often large and showy, and species of *Hibiscus* L., *Althaea* L., *Abutilon* Adans., and other genera are extensively cultivated as ornamentals.

At present 17 genera are represented in Panama. The genus *Modiola* Moench, although not yet reported from Panama, is likely to be found there for *M. caroliniana* (L.) G. Don is widely distributed as a weed in all warmer parts of the world.

Kearney's publication: The American genera of *Malvaceae,* Am. Midl. Nat. **46:** 93-131. 1951, was found very helpful in the preparation of this manuscript.

a. Fruit capsular and loculicidally dehiscent or indehiscent and leathery; staminal tube not filamentiferous at the apex, this commonly dentate or lobed (*Hibisceae*).
- b. Locules of the ovary 1-ovulate; capsules depressed-globose and prominently 5-angulate .... 1. KOSTELETZKYA
- bb. Locules of the ovary 2- to ∞-ovulate; capsules not depressed-globose or prominently angulate.
  - c. Style branches 5, these usually elongate and more or less spreading.
    - d. Calyx regularly 5-dentate or usually 5-lobed, persistent or accrescent .... 2. HIBISCUS
    - dd. Calyx spathaceous, irregularly dentate or lobed, splitting laterally at anthesis, adnate to the base of the corolla and deciduous with it .... 3. ABELMOSCHUS
  - cc. Style unbranched, clavate.
    - e. Epicalyx bractlets large, persistent; capsules loculicidally dehiscent, the pericarp chartaceous to coriaceous, becoming dry and brittle; seeds numerous .... 4. GOSSYPIUM
    - ee. Epicalyx bractlets small, deciduous; capsules indehiscent, leathery; seeds few .... 5. THESPESIA

aa. Fruit a schizocarp.
- f. Style branches and stigmas twice the number of the carpels; staminal tube antheriferous throughout or only on the upper part below the usually dentate or lobulate apex (*Ureneae*).
  - g. Petals auriculate on one side of the claw; immature fruit berrylike, the mericarps enclosed in a fleshy envelope .... 6. MALVAVISCUS
  - gg. Petals not auriculate; fruit not berrylike or fleshy (but the mericarps with a mucilaginous coat in *Pavonia dasypetala* & *P. malacophylla*).
    - h. Leaf veins, at least the midvein, bearing on the back near the base an open, rounded or oblong gland; mericarps dorsally densely glochidiate-echinate .... 7. URENA
    - hh. Leaf veins without a dorsal gland; mericarps not glochidiate-echinate but sometimes muricate or aristate.
      - i. Inflorescences subtended by an involucre of expanded or conduplicate foliaceous bracts, these often whitish or scarious basally in age; epicalyx wanting or the bractlets 9-12 (in *M. radiata*) .... 8. MALACHRA
      - ii. Inflorescences not foliaceous-involucrate or, if so (in *Pavonia* sect. *Peltaea*), the bracts not scarious basally; epicalyx always present .... 9. PAVONIA
- ff. Style branches and stigmas isomerous with the carpels; staminal tube filamentiferous at and often also below the apex (*Malveae*).
  - j. Stigmas introrsely decurrent on the filiform style branches .... 10. MALVA
  - jj. Stigmas apical or very nearly so, capitate, discoid or obliquely truncate, usually distinctly larger than the apex of the style branches.

k. Carpels 1-ovulate.
  l. Epicalyx of 3 distinct bractlets; ovules erect or ascending ....11. MALVASTRUM
  ll. Epicalyx wanting (but a false epicalyx of narrow bracts borne shortly below the calyx present in *Sida ciliaris* & *S. quinquenervia*); ovules pendulous or resupinate-horizontal.
    m. Petals purple or bluish; mericarps with the lateral walls evanescent, the endocarp detached from the pericarp and forming a partial envelope around the seed ....12. ANODA
    mm. Petals commonly yellow or orange; mericarps with the lateral walls persistent, the endocarp not detached from the pericarp ....13. SIDA
kk. Carpels with 2 or more ovules.
  n. Mericarps more or less completely divided into 2 superposed cavities.
    o. Mericarps divided by transversal or oblique constriction of the lateral walls ....14. WISSADULA
    oo. Mericarps divided by a transversal, membranous, tongue-like projection of the dorsal wall (endoglossum) ......15. PSEUDABUTILON
  nn. Mericarps 1-celled.
    p. Mericarps with 2 stout, deflexed, basal, dorsal awns ....16. NEOBRITTONIA
    pp. Mericarps muticous at the base ....17. ABUTILON

1. KOSTELETZKYA Presl

KOSTELETZKYA Presl, Rel. Haenk. **2:** 130. 1835.

Herbs or somewhat shrubby plants, pubescent with small, stellate and/or long, rigid, simple or stellate hairs. *Leaves* petiolate, stipulate, the blade entire to 5-parted, sometimes more or less hastate or sagittate. *Flowers* solitary in the axils or in open, axillary or terminal panicles or racemes; epicalyx of 5 to 10 narrow bractlets, persistent, rarely obsolete; calyx cupuliform, 5-parted, persistent; petals erect or spreading, often pubescent outside; staminal tube elongate, usually 5-dentate, the anthers numerous, reniform; ovary 5-loculate, each locule 1-ovulate, the ovules ascending; style branches 5, the stigmas capitate. *Capsules* depressed-globose, prominently 5-angled, loculicidally dehiscent; seeds reniform.

A genus of about 12 species in Africa, America, Asia and in the Mediterranean region, with only one species reported from Panama.

1. KOSTELETZKYA PENTASPERMA (Bert. ex DC.) Griseb., Fl. Brit. W. Ind. Isl. 83. 1859.

Hibiscus pentaspermus Bert. ex DC., Prodr. **1:** 447. 1824.
Kosteletzkya hastata Presl, Rel. Haenk. **2:** 130. 1835.
K. sagittata Presl, loc. cit. 131, *pl. 70.*
K. hispida Presl, loc. cit. 132.
K. cordata Presl, loc. cit.
Hibiscus tampicensis Moric., Mém. Soc. Phys. Hist. Nat. Genève **7:** 260, *pl. 14.* 1836.
Kosteletzkya stellata Fernald, Bot. Gaz. **20:** 532. 1895.
K. tampicensis (Moric.) Rose, Contr. U. S. Nat. Herb. **8:** 319. 1905.
K. violacea Rose, loc. cit. 319, *pl. 68.*

Herb or shrub, the stem erect, branched, 1-3 m tall, more or less densely pubescent with minute, stellate and longer, stiff, patent, simple or stellate hairs. *Leaves*

short- (uppermost leaves) to long-petiolate (lowest ones), the petiole slender, up to 6 cm long, with the same indumentum as the stem, the stipules subulate, 4-5 mm long; blade polymorphic, from subcircular to linear, simple to 3- to 5-palmatiparted, the base rounded, truncate, cordate or hastate to sagittate (commonly in Panamanian collections), the apex (of blade or lobes) acute to acuminate, the margins irregularly serrate to serrate-dentate, up to 11 cm long, 3- to 7-palminerved, stellate-puberulus and with scattered, longer, appressed, simple or 3-forked hairs on both surfaces, the venation prominent beneath. *Flowers* solitary in the axils of the uppermost leaves, mostly long-pedicellate, the pedicel slender, articulated below the apex, stellate-hispidulous and with few, longer, mostly simple, stiff hairs; epicalyx bractlets narrowly oblong-ovate, acute, 2-3.5 mm long and ca 0.5 mm broad, hispidulous; calyx 3-5 mm long, stellate-puberulus and strigose with long, mostly 3-forked hairs, lobed usually to below the middle, the lobes ovate, acute; petals obovate-cuneate, rounded at the apex, 10-13 mm long, yellow or white, strigose with mostly 3-forked hairs outside; staminal tube ca 7-8 mm long, antheriferous on the upper part; style exceeding slightly the staminal tube, the branches ca 1-1.5 mm long. *Capsule* ca 4-5 mm high and 8-10 mm in diam, the valves stellate-puberulus to stellate-tomentellous, the margins (or the angles) ciliate-hispid with more or less uncinate-tipped hairs; seeds ca 2.5 mm long, sparsely and minutely stellate-scabridulous.

West Indies and Mexico to Venezuela and Ecuador; wet places.

HERRERA: Santa Maria, *Dwyer 4047* (MO). PANAMA: between Las Sabanas and Matías Hernández, *Standley 31912* (US); nr the big swamp E of the Río Tocumen, *Standley 26498* (US); Cerro Azul, alt 500 m, *Dwyer 3084* (MO).

With Bentham (Pl. Hartweg. 114. 1843) and Standley & Steyermark (Fieldiana: Bot. **24**(6): 355. 1949), I consider leaf variation an inadequate character to divide this taxon, because complete intergradation occurs.

2. HIBISCUS L.

Hibiscus L., Sp. Pl. 693. 1753.

Paritium St.-Hil. *et al.*, Fl. Bras. Merid. **1**: 255. 1828.
Wercklea Pittier & Standley, Contr. U. S. Nat. Herb. **18**: 112. 1916.

Herbs, annual or perennial, or shrubs or infrequently small to medium-sized trees, the indumentum of simple or stellate hairs, sometimes aculeate. *Leaves* petiolate, the blade simple to palmatilobed or palmatiparted, the venation palmate, sometimes with a dorsal gland near the base of the midrib. *Flowers* axillary, solitary or forming racemose, paniculate or fasciculate inflorescences, medium or large and showy, the pedicels often articulated; epicalyx usually of numerous bractlets, rarely 2-5 bractlets, occasionally absent or very minute, the bractlets distinct or more or less united at the base, sometimes adnate to the base of the calyx, generally persistent or even accrescent; calyx 5-merous, cupuliform, campanulate or tubular, dentate or lobed, the midvein of each lobe sometimes bearing a gland, generally persistent or even accrescent; petals contorted, more or less unguiculate, adnate to the base of the staminal tube, variously colored; staminal tube usually elongate,

shorter to longer than the corolla, antheriferous throughout or only on the upper part below the 5-lobulate or truncate apex, the filaments long and spreading or short (anthers subsessile); anthers numerous, reniform or hippocrepiform; ovary (4-)5-locular, with 3 to many ovules in each locule, the ovules anatropous (sometimes amphitropous?); style branches 5, these slender and mostly spreading; stigmas capitate, papillate or fimbrillate. *Fruit* a loculicidally dehiscent capsule generally surrounded by the persistent or accrescent epicalyx and calyx; seeds subglobose to reniform, sometimes angulate, glabrous or variously pubescent.

A very large genus widely distributed in subtropical and tropical regions of both hemispheres, and with a few species in temperate zones. Many of the species of *Hibiscus* are extensively cultivated as ornamentals. At present 14 species are reported from Panama.

The following publications were found helpful in preparing the treatment of the genus *Hibiscus:*

Bates, D. M., Notes on cultivated *Malvaceae.* I. *Hibiscus.* Baileya **13:** 56-96, *figs. 19-28.* 1965.

Hochreutiner, B. P. G., Revision du genre *Hibiscus.* Ann. Conserv. Jard. Bot. Genève **4:** 23-191. 1900.

Kearney, T. H., A tentative key to the North American species of *Hibiscus* L. Leafl. West. Bot. **7:** 274-284. 1955.

———, A tentative key to the South American species of *Hibiscus* L. Leafl. West. Bot. **8:** 161-180. 1957.

a. Staminal tube shorter than to equalling more or less the corolla.
  b. Epicalyx bractlets simple or infrequently with a small tooth-like appendage on the inner surface below the apex (cf. *H. radiatus*).
    c. Epicalyx bractlets filiform to ovate or spatulate.
      d. Epicalyx bractlets filiform to ovate.
        e. Corolla 3-12.5 cm long.
          f. Shrubs or trees; leaves entire or with the margin crenulate or dentate.
            g. Leaves entire or with the margin minutely crenulate; staminal tube antheriferous throughout; capsule ovoid or subglobose, 1.5-3.5 cm long; petals yellow or sometimes orange; maritime .... 1. H. TILIACEUS
            gg. Leaves dentate at the margins; staminal tube antheriferous on the upper part; capsule ellipsoid or oblong-cylindric, 5-6.5 cm long.
              h. Branchlets, leaves, pedicel and epicalyx with stellate trichomes; calyx stellate-puberulus to stellate-velutinous and sparsely bristly, the bristles pustular-based, persistent or rarely slightly accrescent; petals obovate or narrowly obovate, 8-12.5 cm long and 4-6 cm wide.
                i. Pedicel 5-16 cm long; epicalyx 6- to 10-lobate nearly to the base, persistent; calyx 2.8-3.8 cm long; petals yellow; staminal tube glabrous .... 2. H. WOODSONII
                ii. Pedicel 26-30 cm long; epicalyx 7-lobate to about the middle, deciduous and leaving a conspicuous scar at the base of the calyx; calyx 4.5-5.5 cm long; petals rose-red; staminal tube pilose below .... 3. H. COCLEANUS

hh. Branchlets, leaves, pedicel, epicalyx and calyx shortly stellate-puberulus and sparsely aculeate to densely hispid-echinate; calyx much accrescent and up to 13 cm long in fruit; petals yellow (sometimes red?), linear-spatulate, 6-8 cm long and 0.8-1.3 cm wide .... 4. H. FEROX

ff. Herbs; mature leaves (some or all) palmatilobed to far below the middle.

j. Calyx becoming dark red or purple and fleshy in fruit, each lobe usually with an elongate gland on the midvein; epicalyx bractlets linear-ovate; plants unarmed .... 5. H. SABDARIFFA

jj. Calyx scarious and greenish or whitish, eglandular; epicalyx bractlets linear and usually with a small tooth-like appendage on the inner surface below the slightly dilated apex; plants sparsely aculeolate .... 6. H. RADIATUS

ee. Corolla 1.4-2 cm long .... 7. H. PHOENICEUS

dd. Epicalyx bractlets spatulate .... 8. H. SPATHULATUS

cc. Epicalyx bractlets linear and abruptly dilated at the apex into a broad, more or less reniform blade .... 9. H. SORORIUS

bb. Epicalyx bractlets clearly bifurcate at the apex.

k. Midvein of each calyx lobe provided with an oblong gland.

l. Plants aculeolate; leaves, at least the lower ones, 3(-5)-lobed mostly to below the middle; epicalyx bractlets longer than the calyx .... 10. H. BIFURCATUS

ll. Plants unarmed; leaves not lobed or sometimes 3-angulate to shallowly 3(-5)-lobed; epicalyx bractlets shorter than the calyx .... 11. H. FURCELLATUS

kk. Midvein of each calyx lobe eglandular; leaves not lobed or sometimes 3-angulate; epicalyx bractlets slightly shorter than the calyx .... 12. H. COSTATUS

aa. Staminal tube much longer than the corolla.

m. Epicalyx bractlets 5-7, 0.7-1 cm long; petals entire to more or less deeply rounded-crenate at the margin .... 13. H. ROSA-SINENSIS

mm. Epicalyx wanting or the bractlets very minute; petals deeply pinnately dissected into numerous oblong or spatulate lobes .... 14. H. SCHIZOPETALUS

1. Hibiscus tiliaceus L., Sp. Pl. 694. 1753.—Fig. 1, 2(A).

H. abutiloides Willd., Enum. Pl. Hort. Reg. Berol. 736. 1809.
Paritium tiliaceum (L.) St.-Hil. *et al.*, Fl. Bras. Merid. **1** : 256. 1828.

Shrub or tree 2-13 m high, evergreen, the branchlets minutely stellate-tomentellous to stellate-puberulus. *Leaves* rather long-petiolate, the petiole terete, up to 14.5 cm long, minutely stellate-tomentellous to stellate-puberulus, the stipules large, oblong-ovate, semiamplexicaul, acute, stellate-tomentellous, early caducous and leaving a conspicuous annular scar around the branches; blade circular or nearly so, deeply cordate at the base, usually abruptly short-acuminate at the apex, generally entire or sometimes minutely crenulate at the margin, up to 19 cm long and 18.5 cm wide, coriaceous, strongly discolor, 7- to 9(-11)-palminerved, the upper surface green when fresh, brown when dry and glabrescent, the lower surface grayish-stellate-tomentellous, with prominent venation and commonly with an elongate open gland at the base of the median vein or of the 3 central veins. *Flowers* axillary, solitary or in few-flowered clusters at the end of the branchlets, the pedicel short, stout, 0.5-1.8 cm long, stellate-tomentellous; epicalyx cupuliform,

Fig. 1. HIBISCUS TILIACEUS L.: A, habit (× ⅔); B, flower (× ⅔); C, androecium, longitudinal section, and pistil (ovary in longitudinal section) (× 1⅓). A after *Allen* 733; B, C after *von Wedel 2729.*

irregularly 8- to 11-lobed, 1.4-2 cm long, stellate-tomentellous, the lobes acute, 0.5-1.5 cm long; calyx cupuliform, lobed to below the middle, 2.2-3 cm long, stellate-tomentellous, the lobes narrowly ovate, acute, 1.3-2.2. cm long, 3-nerved; petals obovate to broadly obovate, cuneiform at the base, rounded at the apex, (4-)5-8 cm long, bright yellow or sometimes orange, fading greenish or reddish, often blackish when dry; staminal tube up to 3.7 cm long, antheriferous throughout, the filaments ca 0.6-0.7 cm long; style ca 1 cm longer than the staminal tube, the branches ca 0.5 cm long, the stigmas densely fimbrillate. *Capsule* surrounded by the persistent epicalyx and calyx, ovoid or subglobose, apiculate, 1.5-3.5 cm in diam, the valves stellate-tomentellous; seeds reniform, ca 4-4.5 mm long, minutely papillate.

A very variable species widely distributed on tropical beaches and in mangrove swamps in both hemispheres. In Panama it is known as *majagua*. The bast fibers of the stem are used by the aborigines in making cordage, fishlines, nets and cloth.

BOCAS DEL TORO: vic of Chiriquí Lagoon, *von Wedel 1349* (MO), *1939* (MO, US); Water Valley, *von Wedel 837* (MO), *1795* (MO, US); Isla Colon, *von Wedel 90* (MO), *516* (MO); Shepherd Island, *von Wedel 2729* (MO, US); Tidal flat nr Garey Creek southeast of Almirante across bay, *McDaniel 5150* (MO); lower Changuinola River, *Dunlap 133* (F), *Stork 133* (US). CANAL ZONE: Fort Sherman, *O. F. Cook s. n.* (US), *Dwyer & A. Robyns 170* (MO); nr Fort Sherman, *Standley 31154* (US); nr Fort Randolph, *Standley 28754* (US); nr Thatcher ferry, *P. White 85* (MO); nr Farfan, *Stern & Chambers 28* (F, MO, US); Venado Beach, Point Brujas, nr Fort Kobbe on Pacific Coast, *Welch 19847* (MO). CHIRIQUÍ: vic of Puerto Armuelles, alt 0-75 m, *Woodson & Schery 810* (MO, US). COLÓN: France Field, *Stevens 1323* (US); Maria Chiquita, *Ebinger 453* (MO); between Fató and Playa de Damas, *Pittier 3939* (US). DARIEN: Puerto St. Dorotea, *Dwyer 2233* (MO), *2234* (MO). PANAMA: Old Panama, *Christopherson 175* (US); San Carlos, *Allen 733* (MO, US), 1134 (MO, US); Punta Paitilla, *Standley 26309* (US); nr Chepo, *Kluge 42* (F, US); Taboga Island, *Bro. Celestine 90* (US), *Miller 1960* (US); Isla Taboguilla, *Duke 5874* (MO); Isla de Pedro Gonzales, *Allen 2585* (MO), *Dwyer 1714* (MO); San José Island, *Erlanson 11* (GH, US), *Johnston 246* (GH); Islas de Perlas, *Johansen 119* (US). SAN BLAS: plain of Sperdi, nr Puerto Obaldia, nr sea level, *Pittier 4361* (US). VERAGUAS: Isla de Coiba, *Mendez 141* (MO).

2. HIBISCUS WOODSONII A. Robyns, Ann. Missouri Bot. Gard. **52:** 179, *fig. 1.* 1965.—Fig. 2 (B).

Wercklea lutea sensu Standley, Ann. Missouri Bot. Gard. **27:** 319. 1940, and sensu Brizicky *et al.*, Trop. Woods **109:** 72. 1958, non Rolfe (1921).

Tree 10-20 m tall, the trunk 30-35 cm in diam, the branchlets stellate-villous-arachnoid. *Leaves* long-petiolate, terete, the petiole often constricted at the base, up to 19 cm long, stellate-tomentellous to stellate-puberulus, the stipules broadly ovate, subacute, stellate-velutinous; blade subcircular or circular, sometimes shallowly angulate, cordate at the base, irregularly and coarsely dentate at the margin, up to 28 cm long and wide, discolor, stellate-puberulus on both surfaces, 7- to 9-palminerved, the main veins prominent especially beneath. *Flowers* axillary, solitary, the pedicel terete, sometimes constricted at the base, 5-16 cm long, stellate-tomentellous to stellate-puberulus, the fruiting pedicel much thickened; epicalyx 1.7-2.2 cm long, 6- to 10-lobate almost to the base, the lobes ovate, acute, the margin extrorsely recurved, up to 1 cm wide, stellate-tomentellous to stellate-puberulus, persistent; calyx campanulate, lobed, prominently 15-nerved, 2.8-3.8 cm long, per-

sistent or sometimes slightly accrescent, stellate-tomentellous or stellate-puberulus and sparsely setiferous, the setae long, mostly simple or infrequently bifurcate, pustular-based, the lobes triangular, acute and 1.3-1.7 cm long; petals obovate, cuneate-unguiculate at the base, rounded at the apex, 8-12.5 cm long and 5-6 cm wide, pale yellow; staminal tube gradually enlarged toward the base, 5-undulate-lobulate at the apex, ca 7 cm long, glabrous, antheriferous on the upper $1/5$; style slightly longer than the staminal tube, the stigmas densely fimbrillate. *Capsule* surrounded by the persistent epicalyx and calyx, ellipsoid, prominently 5-angulate, 5-6.5 cm long, long-acuminate, the acumen ca 1-1.5 cm long, the valves concave, subligneous, densely hispid, the hairs pustular-based; seeds reniform, ca 3-4 mm long, villous.

Native to the Province of Chiriquí, Panama, where it is known as *mompala amarilla* or *amapala amarilla*. The bast is used for making rope and the flowers are reported to have a very fragrant perfume.

CHIRIQUÍ: valley of upper Río Chiriquí Viejo, vic of Monte Lirio, *G. White 41* (MO); id., nr El Volcán, *P. White 175* (F, MO); slopes of Volcán Barú, nr Cerro Punta, alt 6000 ft, *Stern & Chambers 77A* (Y); vic of Bajo Chorro, alt 1900 m, *Woodson & Schery 604* (holotype US, isotype MO); Palo Alto, just E of Boquete, elev 5000 ft, partly disturbed forest of cloud-forest type, *Stern et al. 1087* (MO, US).

3. HIBISCUS COCLEANUS A. Robyns, Ann. Missouri Bot. Gard. **52:** 176. 1965.

Shrub ca 8 m high, the branchlets stellate-villous-arachnoid. *Leaves* very long-petiolate, the petiole terete, constricted near the base, 15-20 cm long, more or less densely stellate-villous-arachnoid, the stipules broadly triangulate, obtuse, stellate-velutinous; blade subcircular, cordate at the base, more or less acute at the apex, irregularly dentate at the margin, ca 21-24 cm long and wide, thick-chartaceous, discolor, 9-palminerved, the upper surface scabrous, sparsely stellate-puberulus but stellate-tomentellous along the main veins, the lower surface softly stellate-velutinous, the veins prominent especially beneath. *Flowers* axillary, solitary, the elongate pedicel constricted near or at the base, 26-30 cm long, more or less densely stellate-villous-arachnoid; epicalyx cupuliform-campanulate, 7-cleft to about the middle, ca 2.5 cm long, densely stellate-velutinous, deciduous and leaving a conspicuous scar at the base of the calyx, the lobes ovate and acute; calyx campanulate, lobed, prominently 15- or 20-nerved, 4.5-5.5 cm long, densely stellate-velutinous and with scattered, long, simple or bifurcate or trifurcate, pustular-based, hispid hairs, the lobes ovate-triangular, acuminate and 2.5-3 cm long; petals narrowly obovate, attenuate at the base, rounded at the apex, ca 12 cm long and 4 cm wide, rose-red; staminal tube gradually enlarged toward the base, ca 10 cm long, sparsely pilose especially below, antheriferous on the upper $1/5$; style slightly longer than the staminal tube, the stigmas densely fimbrillate. *Capsule* unknown.

Native to the Province of Coclé, Panama.

COCLÉ: El Valle, *Dwyer 1918* (holotype MO).

4. HIBISCUS FEROX Hook., Curt. Bot. Mag. **74:** *t. 4401*. 1848.—Fig. 2 (C,D).

Shrub or small tree up to at least 6 m high, the branches and branchlets stellate-puberulus and sparsely aculeate, the prickles short, straight and stout. *Leaves*

long-petiolate, the petiole stout, constricted at the base, up to 34 cm long, sparsely stellate-pubescent and aculeate, the stipules very large and foliaceous; blade circular or nearly so, deeply cordate at the base, rounded at the apex, coarsely and sharply dentate or dentate-echinulate at the margin, up to 42 cm in diam, membranous, slightly discolor, appressed-stellate-puberulus and sparsely aculeate especially along the veins on both surfaces, the indumentum denser beneath, 5- or 7-palminerved, the venation impressed above and prominent beneath. *Flowers* crowded toward the apex of the branchlets, axillary, in few-flowered fascicles, the pedicels short to long, shortly stellate-puberulus and hispid-echinate, the fruiting pedicel up to 16 cm long; epicalyx of 7-10 bractlets, these narrowly ovate, almost free to the base, acute at the apex, 2.5-3.7 cm long and 0.5-0.9 cm wide, stellate-puberulus and hispid-echinate or not, accrescent; calyx tubular, dentate, 10-nerved, 2.5-5 cm long, much accrescent and up to 13 cm in fruit, fleshy and red, stellate-puberulus and densely hispid-echinate, the teeth deltoid and 0.5-1 cm long; petals linear-spatulate, spreading above, 5-8 cm long and 0.8-1.3 cm wide, yellow; staminal tube shorter than or equalling the corolla, antheriferous on the upper part; style slightly longer than the staminal tube, the stigmas densely fimbrillate. *Capsule* enveloped by the much-accrescent calyx, oblong-cylindric, 5-angulate, ca 5 cm long, the valves rigid-chartaceous, strongly reticulate-veined, nearly glabrous; seeds reniform, ca 2.5 mm long, minutely puberulus.

Costa Rica to Colombia; along river banks, in clay or gravelly wet soil.

CANAL ZONE: Alhajuela, Río Chagres, *Pittier 2345* (US); between Peluca Hydrographic Station and Quebrada Peluca, along Río Boqueron, *Steyermark* & *Allen 17223* (MO). COLÓN: Río Viejo, vic of Puerto Pilon, alt 10 m, *Allen 4098* (MO). DARIEN: Caná and vic, elev 2000-6500 ft, *R. S. Williams 819* (US).

5. Hibiscus sabdariffa L., Sp. Pl. 695. 1753.

Herb, annual, 0.5-2 m high, the stem glabrous or sparsely puberulus. *Leaves* long-petiolate, the petiole up to 6.5 cm long, glabrous or sparsely puberulus, the stipules narrowly triangular, acute; blade polymorphic, simple and ovate-acute to usually 3- to 5- to 7-palmatifid, the lobes verry narrowly elliptic and acute, with acute sinuses, serrulate or crenulate at the margin, up to 12-15 cm long, glabrous, the midrib prominent and bearing a subbasal gland beneath. *Flowers* axillary, solitary or in racemiform, terminal inflorescences by reduction of the upper leaves, the pedicel short and stout, 5-7 mm long; epicalyx of ca 10 bractlets, these linear-ovate, united basally and adnate to the base of the calyx, ca 8-12 mm long, sparsely hirsute especially toward the base, accrescent; calyx cupuliform, lobed to about or to below the middle, 1.5-2.2. cm long, deep red, much accrescent, up to 3.5 cm long in fruit and becoming with the epicalyx fleshy and dark red or purple, the lobes ovate, acute, strongly 3-nerved, usually with an elongate gland on the midvein of each lobe, sparsely hirsute especially toward the base; petals cuneate-obovate, rounded at the apex, 3-5 cm long, cream-colored or yellow, often tinged with red; staminal tube much shorter than the corolla. *Capsule* much shorter than the accrescent calyx, subglobose, apiculate, 1.8-2 cm long, appressed-hirsute; seeds reniform-angulate, 3-5 mm long, very minutely puberulus.

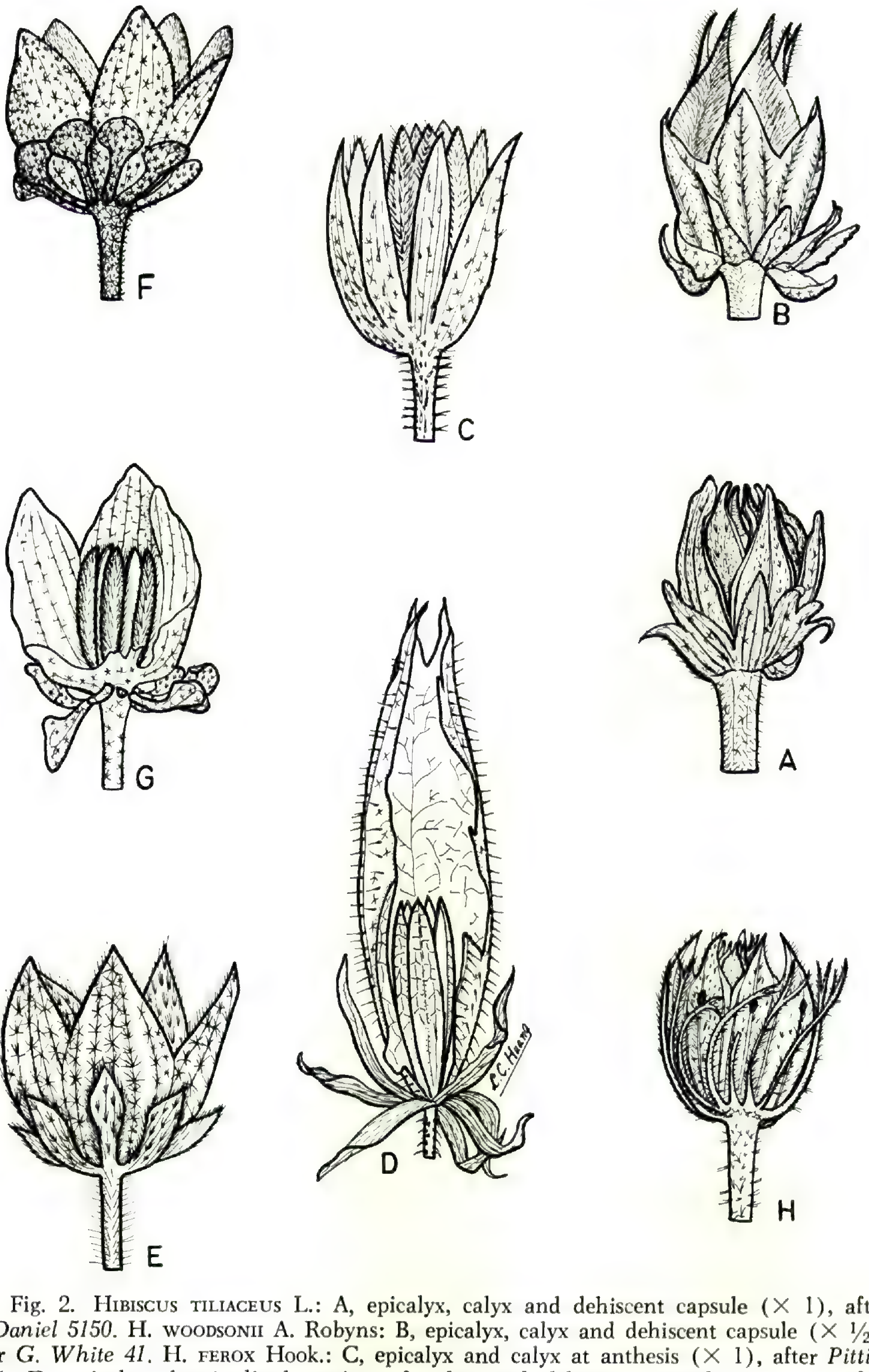

Fig. 2. HIBISCUS TILIACEUS L.: A, epicalyx, calyx and dehiscent capsule (× 1), after *McDaniel 5150*. H. WOODSONII A. Robyns: B, epicalyx, calyx and dehiscent capsule (× ½), after *G. White 41*. H. FEROX Hook.: C, epicalyx and calyx at anthesis (× 1), after *Pittier 2345;* D, epicalyx, longitudinal section of calyx and dehiscent capsule (× ½), after *Steyermark & Allen 17223*. H. SPATHULATUS Garcke: E, epicalyx and calyx (× 1), after *Pittier 4054*. H. SORORIUS L. f.: F, epicalyx and calyx (× 1), G, epicalyx, longitudinal section of calyx and dehiscent capsule (× 1), after *Seibert 634*. H. BIFURCATUS Cav.: H. epicalyx, calyx showing the gland on the midrib of each lobe, and capsule apex (× 1), after *Pittier 3997*.

Roselle or Jamaica Sorrel is cultivated throughout the tropics and is often naturalized. The fleshy epicalyx and calyx are used for making preserves and a beverage simulating lemonade. It is called *viñuela* in Panama (cf. *Standley* 25222).

CANAL ZONE: Corozal, cult. plant, *J. M. & M. T. Greenman 5192* (MO); Sosa Hill, Balboa, edge of clearing, commonly cult. and also wild, *Standley 25222* (US).

6. HIBISCUS RADIATUS Cav., Mon. Cl. Diss. Dec. 150, *t. 54(2)*. 1787.

H. unidens Lindl., Bot. Regist. *pl. 878*. 1825.
H. cannabinus L. var. *unidens* (Lindl.) Hochr., Ann. Conserv. Jard. Bot. Genève **4:** 115. 1900.

Herb, annual, up to 2-3 m high, the stem simple or branched, sparsely aculeolate, the prickles pustular-based and upturned, otherwise glabrous or with a longitudinal short-hairy line changing radially at each node. *Leaves* with slender elongate petioles, these with the same indumentum as the stem, the stipules filiform; blade polymorphic, simple and more or less subcircular to usually 3- to 5(-7)-palmatifid, the lobes elliptic to linear-ovate and acute or acuminate, serrate at the margins, up to 15 cm long, glabrate or with few minute prickles on the veins. *Flowers* axillary, solitary or in racemiform terminal inflorescences by reduction of the uppermost leaves, subsessile or short-pedicellate, the pedicel stout, up to 5 mm long and aculeolate; epicalyx of 7-10 bractlets, these linear, channelled, united at the base and adnate to the base of the calyx, flattened and slightly dilated at the apex, usually with a small tooth-like appendage on the inner surface below the apex, 8-15 mm long, setose especially along the margins, the setae hyaline and pustular-based; calyx cupuliform, lobed to below the middle, 15-25 mm long, up to 30 mm in fruit, scarious, greenish or whitish, setose, the lobes long-acuminate, 3-nerved, eglandular; petals cuneate-obovate, rounded at the apex, 3.5-8 cm long, yellow or red, with crimson basal spots; staminal tube about ½ as long as the corolla, antheriferous on most of its length, the filaments mostly paired; style about as long as the staminal tube, the stigmas densely fimbrillate. *Capsule* surrounded by the persistent epicalyx and calyx, ovoid, acuminate, 15-20 mm long, densely appressed-setose, the valves ligneous; seeds subreniform-angulate, 3-5 mm long, very minutely appressed-squamose.

A fiber plant native to southeastern Asia, but now widespread in tropical and subtropical regions and sometimes cultivated for ornament.

PANAMA: Juan Díaz, cult., *Standley 30526* (US).

Hibiscus radiatus is very similar to *H. cannabinus* L., from which it is distinguished by the absence of an elongate gland near the base of the midrib on the lower leaf surface and on the midvein of each calyx lobe, by the presence, in most cases, of a small tooth-like appendage below the apex on the inner surface of the epicalyx bractlets, and by the lack of a whitish tomentellum on the calyx. Furthermore, cytological data presented by Menzel & Wilson (Am. J. Bot. **48:** 651-657. 1961) support the specific separation of these two taxa (see also Bates, Baileya **13:** 81-82. 1965).

7. HIBISCUS PHOENICEUS Jacq., Hort. Bot. Vindob. **3:** 11, *t. 14.* 1776.

Herb or suffrutex 0.6-1.5 m high, the stem almost glabrous or sparsely appressed-stellate-hispidulous, sometimes also with a longitudinal tomentellous line changing radially at each node. *Leaves* with a slender petiole 0.5-2 cm long, with the same indumentum as the stem, the stipules filiform; blade deltoid-ovate or narrowly deltoid-ovate, often subhastately or rarely deeply 3-lobed, subcuneate or obtuse or truncate or rarely slightly subcordate at the base, acute to acuminate at the apex, crenate-serrate at the margins, up to 9 cm long, minutely stellate-puberulus to glabrescent above, appressed-stellate-hispidulous beneath, usually 5-palminerved, the main veins prominent on both sides but especially beneath. *Flowers* axillary, solitary, the pedicel slender, articulated, 1-5 cm long, appressed-stellate-hispidulous; epicalyx of about 10 bractlets, these linear, acute, equalling more or less the calyx or often much longer and up to 25 mm long, appressed-stellate-hispidulous, ciliolate at the margin; calyx lobed to far below the middle, 7-12 mm long, appressed-stellate-hispidulous, the lobes ovate to narrowly ovate, acute; petals cuneate-obovate, rounded at the apex, 1.4-2 cm long, crimson or rarely white, appressed-stellate-hispidulous outside; staminal tube shorter than or more or less equalling the corolla, antheriferous throughout; style branches exceeding the staminal tube, the stigmas densely fimbrillate. *Capsule* subglobose, apiculate, equalling more or less the persistent calyx, appressed-hispidulous, the hairs simple; seeds subreniform-angulate, 2-3 mm long, covered with long, white hairs.

West Indies and Mexico to Colombia and Venezuela; in open forest and shrub.

PANAMA: Taboga Island, *Sinclair s.n.* (cf. Hemsl., Biol. Centr.-Am. **1**: 122. 1879).

Hibiscus phoeniceus is often considered as a synonym for *H. brasiliensis* L. (Sp. Pl. ed. 2, 977. 1763) (cf. Hochreutiner, Ann. Conserv. Jard. Bot. Genève **4:** 87-90. 1900). As the short protologue of Linnaeus, however, does not agree with the description and the illustration of *H. phoeniceus*—especially with regard to the shape of the leaves—I now consider Linnaeus' specific epithet as a *nomen dubium.*

8. HIBISCUS SPATHULATUS Garcke, Bot. Zeit. **7**: 840. 1849, non *Lagunaea spathulata* Gaudichaud (Bot. in Freycinet, Voyage autour du Monde 476. 1830).—Fig. 2 (E).

H. verbasciformis Klotzsch ex Schomb., Reisen in Britisch-Guiana 991. 1848, nom. nud.

Herb up to 2 m high, the stem densely hirsute with long, stellate hairs. *Leaves* short- to long-petiolate, the petiole terete, 1-11 cm long, densely stellate-hirsute, the stipules subulate-filiform; blade broadly ovate to subcircular, often 3- to 5-angulate or slightly 3-lobed, more or less cordate at the base, acute at the apex, irregularly dentate at the margin, up to 10-20 cm long, 5- to 7-palminerved, stellate-hirsute on both sides but the indumentum always denser beneath, the nervation slightly prominent beneath. *Flowers* solitary in the upper leaf axils, the pedicel 9-16 cm long, densely stellate-hirsute; epicalyx of 9-10 bractlets, these spatulate to narrowly spatulate, acute or more or less obtuse, 1-1.7 cm long and 0.3-0.55 cm wide, densely stellate-hirsute; calyx campanulate, lobed to about or to slightly below the middle, 2.2-2.6 cm long, accrescent and up to 3 cm long in fruit, densely

stellate-hirsute, the lobes deltoid-ovate to broadly deltoid-ovate, acute to acuminate; petals obovate, 4-5.5 cm long, pink or purplish; staminal tube 30-35 mm long, antheriferous throughout; style branches exceeding the staminal tube. *Capsule* surrounded by the accrescent calyx, more or less globose, shortly mucronulate at the apex, 1-1.2 cm long, densely stellate-hispid; seeds subreniform-angulate, 1.7-1.8 mm long, very minutely papillate.

Panama, British Guiana and northern Brazil.

CANAL ZONE: nr old Fort Lorenzo, mouth of Río Chagres, *Piper 5896* (US); Cuatro Calles Hills, nr Matachin, alt 20-150 m, *Pittier 4054;* Río Paraíso, above East Paraíso, wet thicket, *Standley 29841* (US). VERAGUAS: hills W of Soná, alt ca 500 m, *Allen 1019* (F, MO).

9. Hibiscus sororius L. f., Suppl. Pl. Syst. Veg. 311. 1781.—Fig. 2 (F, G).

H. sororius f. *albiflorus* Standley, Contr. Arnold Arb. **5:** 101. 1933.

Herb or suffrutex up to 2 m high, the stem sparsely to densely scabridulous-puberulus with appressed stellate hairs. *Leaves* with the petiole terete, 1.5-11 cm long, densely scabridulous-puberulus with appressed stellate hairs, the stipules small, linear below and abrupty dilated at the apex into a more or less deltoid blade, velutinous; blade broadly ovate to suborbicular, rarely more or less angulate, deeply cordate at the base, obtuse at the apex, shallowly crenate at the margin, up to 16 cm long and 13 cm wide, 5- to 9-palminerved, scabridulous on both surfaces, stellate-puberulus above, more or less densely appressed-stellate-puberulus and with the venation slightly prominent beneath. *Flowers* solitary in the upper leaf axils, long-pedicellate, the pedicel articulated at or above the middle, up to 12 cm long, scabridulous-stellate-tomentellous; epicalyx of 8-10 bractlets, these linear below and abruptly dilated at the apex into a broad, more or less reniform blade, 0.7-1.5 cm long and 0.55-1.2 cm wide (the blade), scabridulous-stellate-tomentellous; calyx lobed to below the middle, 2-3 cm long, accrescent, scabridulous-stellate-tomentellous to -puberulus, the lobes ovate, obtuse to subacute and 5- or 7-nerved; petals obovate, unguiculate, rounded at the apex, (3.5-)5-7.5 cm long, white or pink with a red center, stellate-puberulus near the apex outside; staminal tube ½ as long as the corolla, antheriferous throughout; style branches exceeding the staminal tube, the stigmas minutely fimbrillate. *Capsule* surrounded by and smaller than the accrescent calyx, broadly oblong-ellipsoid, rounded to slightly retuse and mucronulate at the apex, 1.2-2.5 cm long, densely hispid with long, simple hairs; seeds subglobose-reniform, ca 1.5-1.7 mm long, glabrous to very minutely papillate.

Cuba and Central America to Bolivia and northern Argentina; usually in swamps.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 435* (F). CANAL ZONE: Barro Colorado Island, *Aviles 910* (F), *L. H. & E. Z. Bailey 257* (F), 388 (F), *Bangham 511* (F, US,) *572* (F, US), *Marjorie Brown 89* (F), *Frost 117* (F), *Kenoyer 437* (US), *Shattuck 251* (F), *Starry 122* (F), *Wetmore & Abbe 24* (F), *25* (F, type of *H. sororius* f. *albiflorus*), *100* (F), *187* (F), *188* (F); between Frijoles and Monte Lirio, alt 30 m, *Killip 12183* (US); Gigante Bay, *Dodge 3475* (US), *3477* (US); Darien Station, *Standley 31593* (US). DARIEN: s. loc., *Macbride 2693* (F, US). PANAMA: vic of Arenoso, Río Trinidad, alt 26-50 m, *Seibert 634* (MO).

10. HIBISCUS BIFURCATUS Cav., Mon. Cl. Diss. Dec. 146, *t. 51(1).* 1787.—Fig. 2 (H).

Suffrutex or shrub up to 4 m high, the stem stellate-puberulus or stellate-hirtellous (mostly along longitudinal lines) and aculeolate, the prickles pustular-based and pointed downwards. *Leaves* with the petioles slender, up to 10 cm long, stellate-hirtellous and aculeolate, the stipules linear-subulate; blade cordate at the base, 3(-5)-lobed mostly to below the middle (at least the lower leaves), the lobes ovate to narrowly ovate, the sinuses acute and the apex acuminate, the blade of the upper leaves sometimes sub-3-lobed to simple and obtuse at the base, dentate-serrate at the margin, up to 12 cm long, 5- to 7-palminerved, hirtellous with simple and stellate hairs on both surfaces, the venation slightly prominent beneath, the main veins generally shortly aculeolate and the midvein with a small, basal, elongate gland on the lower surface. *Flowers* solitary in the upper leaf axils, the pedicel articulated, 2-7 cm long, stellate-hirtellous and aculeolate or hispid; epicalyx of 9-13 bractlets, these linear, unequally bifurcate at the apex, ca 2 cm long, hirsute to hispid with pustular-based hairs, slightly accrescent; calyx lobed to the middle or slightly below, (1-)1.4-1.8 cm long, accrescent and up to 2.3 cm long in fruit, hirsute to hispid with pustular-based hairs, the lobes deltoid, acuminate, prominently 3-nerved, the lateral veins very close to the margin (thickened margin), the midvein of each lobe with an oblong gland; petals cuneate-obovate, rounded at the apex, (5-)7-9 cm long, rose, sometimes purple-striate; staminal tube about ½ as long as (to more or less equalling?) the corolla, antheriferous throughout; style branches exceeding the staminal tube, the stigmas hirtellous. *Capsule* surrounded by and slightly shorter than the accrescent calyx, broadly ovoid, acuminate and mucronulate, ca 2-2.2 cm long, the mucro ca 2 mm long, the valves rigid-chartaceous, appressed-sericeous; seeds angulate, 3-4 mm long, sparsely and very minutely papillate.

West Indies and Mexico to Guiana and Brazil.

CANAL ZONE: Barro Colorado Island, *Kenoyer 438* (US); Agua Clara, alt 10-40 m, in inundated places, *Pittier 3997* (US).

11. HIBISCUS FURCELLATUS Desrousseaux in Lam., Encycl. Méth. Bot. **3:** 358. 1789.

Suffrutex 1-2 m high, the stem puberulus to velutinous with minute stellate hairs and sometimes with short prickle-like simple hairs. *Leaves* with the petiole 3-8 cm long, stellate-velutinous, the stipules subulate-filiform; blade broadly ovate, subcircular or depressed ovate, sometimes 3-angulate or shallowly 3(-5)-lobed, cordate at the base, obtuse to acuminate at the apex, irregularly dentate or denticulate at the margin, usually 8-12 cm long and wide, 5- to 9-palminerved, somewhat scabridulous and stellate-puberulus above, stellate-velutinous to stellate-puberulus, with the venation slightly prominent and with an oblong gland near the base of the midrib beneath. *Flowers* solitary in the upper leaf axils, the pedicel stout, articulated, 1-3 cm long, stellate-velutinous and sometimes hispid with long, simple to stellate, pustular-based hairs; epicalyx of 10-14 bractlets, these narrowly linear, unequally bifurcate at the apex, 8-12 mm long, minutely stellate-velutinous and

sometimes hispid with long, simple to stellate, pustular-based hairs, slightly accrescent; calyx cupuliform, lobed to about the middle, 15-20 mm long, accrescent, minutely stellate-velutinous, the lobes deltoid-oblong, acuminate, prominently 3-nerved, the veins mostly hispid with long, simple to stellate, pustular-based hairs, the lateral veins very close to the margin (thickened margin), the midvein of each lobe with an oblong gland; petals cuneate-obovate, rounded at the apex, 6-9 cm long, rose-purple with a darker center; staminal tube ca ½ as long as the corolla, antheriferous throughout; style branches exceeding the staminal tube, the stigmas hirtellous. *Capsule* surrounded by and slightly shorter than the accrescent calyx, broadly oblong-ovoid, acuminate and mucronulate, 22-25 mm long, the mucro ca 2 mm long, the valves minutely stellate-velutinous and sericeous with long, simple, white hairs; seeds subrotund-reniform-angulate, ca 3 mm long, glabrous.

Florida, West Indies and southern Mexico to Brazil and Paraguay.

CANAL ZONE: Chiva-Chiva Trail, *Piper 5722* (US?).

I have not seen the above mentioned collection which was determined and cited as such in Kearney's manuscript (see footnote 2). It was impossible to locate this specimen at the U. S. National Herbarium, Washington, D. C., where Maxon's collections are deposited.

12. HIBISCUS COSTATUS A. Rich., Bot., Pl. Vasc. in Ramon de la Sagra, Hist. Phys. Pol. Nat. Cuba 138. 1845, *t. 15.* 1850 (?).

Herb or suffrutex 1-2 m high, the stem scabrous, stellate-hirsute. *Leaves* with the petiole terete, up to 8.5 cm long, stellate-hirsute, the stipules subulate; blade broadly ovate, sometimes 3-angulate, cordate at the base, acuminate at the apex, serrulate-denticulate at the margin, commonly 6-11 cm long and 5-10 cm wide, usually 7-palminerved, scabrous and hirsute with mostly stellate hairs on both surfaces, the venation slightly prominent beneath, the midrib with or without an oblong gland near the base on the lower surface. *Flowers* solitary in the upper leaf axils, short- to mostly long-pedicellate, the pedicel articulated, up to 10 cm long, stellate-hispidulous; epicalyx of about 10 bractlets, these linear, dilated and unequally bifurcate at the apex, 13-23 mm long, hispid with simple and/or stellate hairs, accrescent; calyx campanulate, lobed to slightly below the middle, 15-25 mm long, accrescent and up to 32 mm in fruit, hispid with simple and/or stellate hairs, the lobes deltoid to narrowly deltoid, long-acuminate, 3-nerved, the lateral veins very close to the margin (thickened margin) and the midvein eglandular; petals cuneate-obovate, 4-8 cm long, pink or purplish; staminal tube about ⅔ as long as the corolla, antheriferous throughout (?); style branches exceeding the staminal tube, the stigmas densely fimbrillate. *Capsule* surrounded by and shorter than the accrescent calyx, ovoid, acuminate and mucronulate at the apex, 22-25 mm long, the mucro ca 2 mm long, the valves rigid-chartaceous, densely stellate-puberulus and long-strigose with simple, white hairs; seeds subrotund-reniform, ca 2.5-3 mm long, glabrous or minutely papillate.

Cuba and Mexico to Panama.

COCLÉ: Bismarck above Penonomé, *R. S. Williams 331* (US).

13. HIBISCUS ROSA-SINENSIS L., Sp. Pl. 694. 1753.

Shrub up to 7 m high, the branchlets glabrous or nearly so. *Leaves* rather short-petiolate, the petiole up to 3 cm long, the stipules lanceolate-subulate; blade ovate, subcuneate, rounded or truncate at the base, acute to more or less long-acuminate at the apex, irregularly and coarsely serrate at the margin, up to 12-15 cm long and 7-9 cm wide, membranous, glabrous or nearly so, 5- or 7-palminerved, the nerves prominent beneath. *Flowers* large, axillary, solitary, the pedicels short to usually elongate and slender, articulated above the midde, up to 12.5 cm long, glabrous or sparsely minutely stellate-puberulus; epicalyx or 5-7 bractlets, these free, narrowly ovate, acute, 0.7-1 cm long, sparsely minutely stellate-puberulus; calyx tubular-campanulate, lobed, 10-nerved, 1.8-2.4(-3) cm long, sparsely minutely stellate-puberulus, the lobes deltoid, acute, 0.5-0.8 cm long; petals broadly cuneate-obovate, rounded at the apex, entire to more or less deeply rounded-crenate at the margin, 8(6-10) cm long, usually bright red; staminal tube exceeding the corolla, long-exserted and up to 11-12 cm long, 5-lobed at the apex, antheriferous on the upper part, the filaments about 6-9 mm long; style about 1 cm longer than the staminal tube, the branches up to 1 cm long, sparsely villous, the stigmas hirtellous. *Capsule* not seen.

Chinese *Hibiscus*, presumably indigenous to eastern Asia, is now one of the most extensively planted ornamentals, often as a hedge plant, in all tropical and subtropical regions; occasionally it escapes and naturalizes. A common name in Panama is *papo* (cf. *Standley 25316 & 30350*).

CANAL ZONE: Frijoles, cut over and cultivated area, *Ebinger 315* (MO); Barro Colorado Island, cult., *Woodworth* & *Vestal 634* (F); vic of Madden Dam, *Dwyer* & *A. Robyns 16* (MO); Balboa, cult., *Maxon 6832* (US). COLÓN: between Catival, Canal Zone, and France Field, brushy slope, wild, *Standley 30350* (US). PANAMA: Panama City, evidently wild in dry sunny sandy jungle adjacent to ocean beach, *Macbride 2611a* (F, US); Bella Vista, coastal thicket, wild, *Standley 25316* (US).

14. HIBISCUS SCHIZOPETALUS (Masters) Hook. f., Curt. Bot. Mag. **106:** *t. 6524.* 1880.

H. rosa-sinensis L. var. *schizopetalus* Masters, Gard. Chron. 1879: 272, *fig. 45;* Boulger, Gard. Chron. 1879: 372.

Shrub up to 4 m high, glabrous or nearly so. *Leaves* rather short-petiolate, the petiole slender, up to 1.7 cm long, canaliculate and stellate-hirtellous above, the stipules subulate-filiform; blade elliptic to narrowly elliptic, acute to obtuse at the base, acute at the apex, serrulate-denticulate at the margin, up to 6 cm long and 2.5 cm wide, glabrous, usually 3-palminerved, the nervation slightly prominent beneath. *Flowers* showy, solitary in the upper leaf axils, pendent, the pedicels very long, slender, articulated near the middle, up to 14 cm long, glabrous to minutely papillate; epicalyx none or the bractlets usually very minute; calyx tubular-campanulate, irregularly lobed, 15-20 mm long, spathaceous, glabrous or minutely papillate; petals reflexed, obovate, long-unguiculate, deeply pinnately dissected into numerous oblong or spatulate lobes, 4-7 cm long, pink or red; staminal tube slender, 5-lobulate at the apex, well exceeding the corolla and up to 9 cm long, antheriferous on the upper part, the filaments up to 7 mm long; style much longer

than the staminal tube, the style branches ca 10-12 mm long, the stigmas fimbrillate. *Capsule* oblong-cylindraceous, obtuse, the seeds glabrous.

A very handsome shrub native to tropical East Africa, extensively cultivated in tropical America and occasionally escaping, but probably nowhere naturalized in this hemisphere; known in Panama as *paraguïta China* (cf. *Standley 30533*).

BOCAS DEL TORO: Old Bank Island, vic of Chiriquí Lagoon, *von Wedel 1859* (MO, US). CANAL ZONE: Summit, cult. plants at the Plant Introduction Garden, *Steyermark s. n.* (MO). PANAMA: Juan Díaz, planted, *Standley 30533* (US).

3. ABELMOSCHUS Medic.

Abelmoschus Medic., Malv.-Fam. 45. 1787.

Herbs or undershrubs, mostly annual, the indumentum commonly hirsute or setose and mostly with simple hairs. *Leaves* long-petiolate, the stipules caducous, the blade angulate to palmatilobed to palmatifid. *Flowers* large, axillary, solitary, sometimes in terminal racemes, pedicellate; epicalyx of 4-∞ distinct bractlets, persistent or caducous; calyx much longer than the epicalyx, spathaceous, irregularly lobed or dentate, splitting laterally at anthesis, circumcissile, adnate to the base of the corolla and deciduous with it; petals obovate, short-unguiculate, adnate to the base of the staminal tube; staminal tube antheriferous from near the base to the apex, the filaments very short; ovary 5-locular, the locules ∞-ovulate; styles shortly 5-branched, the stigmas capitate and hirtellous. *Capsules* usually elongate, acuminate, loculicidally dehiscent, with numerous seeds in each locule; seeds glabrous or pubescent.

An Old World genus of about 20 species, of which the two following are extensively cultivated in the warmer regions of both hemispheres and occasionally escape there, but rarely, if ever, become naturalized in the Americas.

a. Indumentum sparsely setulose or rarely 0; pedicel short, 5-15 mm long, up to 2.5 cm long in fruit; epicalyx bractlets caducous; petals 3-4(-6) cm long; capsule oblong to narrowly oblong-ovate, 5-angulate, 7.5-16 cm long and 1.5-2.5 cm in diam .... 1. A. ESCULENTUS

aa. Indumentum long-hirsute, the hairs on stem, petiole and pedicel spreading or usually retrorse; pedicel up to 4 cm long, up to 10 cm long in fruit; epicalyx bractlets persistent; petals (4-)7-8 cm long; capsule ovoid, 5-7 cm long and 2-3 cm in diam .... 2. A. MOSCHATUS

1. Abelmoschus esculentus (L.) Moench, Method. Pl. 617. 1794.

Hibiscus esculentus L., Sp. Pl. 696. 1753.

Herb or suffrutex, the stem up to 2.5 m high, glabrous or sparsely setulose. *Leaves* with the petiole 5-20 cm long, setulose, the stipules subulate, up to 12 mm long, setulose, early caducous; blade subcircular in outline and up to 20 cm in diam, cuneate to truncate to cordate at the base, palmatilobed, -cleft or -fid, the segments deltoid-ovate to narrowly elliptic or oblanceolate, acute at the apex, finely to coarsely serrate at the margin, 3- or 5(-7)-palminerved, sparsely setulose especially along the prominent veins beneath. *Flowers* solitary in the uppermost leaf

axils, the pedicel stout, terete, enlarged near the apex, 5-15 mm long, up to 2.5 cm long and much thickened in fruit, setulose; epicalyx bractlets 8-12, linear-lanceolate, 12-15 mm long, setulose, caducous; calyx 5-dentate, up to 2.5 cm long, setulose; petals asymmetrical, rounded at the apex, 3-4(-6) cm long, yellow with dark red or purple basal spots; staminal tube about ½ as long as the corolla; styles exceeding slightly the staminal tube. *Capsule* oblong to narrowly oblong-ovate, long-acuminate, 5-angulate, 7.5-16 cm long and 1.5-2.5 cm in diam, densely short-hirsute when young, at length glabrescent; seeds globose-reniform, ca 5 mm in diam, glabrous or minutely stellate-puberulus or sometimes pilose.

Okra or gumbo, the well-known garden vegetable. In Panama, it is called colloquially *najú*, and the seeds are used like coffee and in chocolate (cf. *Standley 25279*).

CANAL ZONE: Balboa, weedy field, wild and cult., *Standley 30891* (US); id., old garden, *Standley 25573* (US); Sosa Hill, Balboa, edge of finca, *Standley 25279* (US). PANAMA: Tocumen, Agronomy School Farm, *Dwyer 1979* (MO).

2. ABELMOSCHUS MOSCHATUS Medic., Malv.-Fam. 46. 1787.

Hibiscus abelmoschus L., Sp. Pl. 696. 1753.

Herb or suffrutex, the stem somewhat woody below, up to about 3 m high, hirsute with long, mostly simple, spreading or retrorse, whitish hairs. *Leaves* with the petiole up to 15 cm long, spreading- or retrorse-hirsute, the stipules subulate, 6-8 mm long, hirsute; blade usually circular or subcircular in outline and up to 20 cm long and 24 cm broad, cordate or sagittate at the base, prominently 5-angulate to usually 3- or 5-palmatilobed or -fid, the segments from deltoid to narrowly oblong-ovate, with the sinuses usually rounded, acute to long-acuminate at the apex, coarsely serrate to serrate-dentate or infrequently nearly entire at the margin, 5- or 7-palminerved, appressed-hirsute and with the venation prominent on both sides. *Flowers* solitary in the uppermost leaf axils, long-pedicellate, the pedicel terete, enlarged near the apex, up to 4 cm long, thickened and up to 10 cm long in fruit, spreading- or usually retrose-hirsute; epicalyx bractlets 8-10, very narrowly ovate, acute, 10-17 mm long and 1-2.5 mm broad, long-ciliate, persistent; calyx 2-3.5 cm long, 5-dentate and with the teeth up to 5 mm long, 15-nerved, appressed-hirtellous; petals asymmetrical, rounded at the apex, (4-)7-8 cm long, yellow with a dark purple spot at the base; staminal tube about ¼-⅓ as long as the corolla; styles exceeding slightly the staminal tube. *Capsule* ovoid, acuminate, 5-7 cm long and 2-3 cm in diam, appressed-hispid; seeds globose-reniform, ca 3-4 mm long, the testa striate.

Musk okra, cultivated in the Old World as a fiber plant and for its musk-scented seeds, which are used in perfumery. Often planted as an ornamental in the American tropics.

BOCAS DEL TORO: 4-6 mi N of Almirante, low open area nr railroad, *McDaniel 5109* (MO); Water Valley, *von Wedel 726* (MO); Shepherd Island, *von Wedel 2676* (MO, US); Changuinola Valley, *Dunlap 272* (F, US). CANAL ZONE: nr Corozal, *Piper 5299* (US); Corozal, brushy slope, *Standley 27394* (US); Las Cascadas Plantation, nr Summit, in ditch, *Standley 29554* (US); s. loc., *Slater s.n.* (F). CHIRIQUÍ: vic of Río Tinta, along highway,

Woodson et al. 400 (MO). COLÓN: between France Field, Canal Zone, and Catival, roadside, *Standley 30362* (US). DARIEN: Río Sabana, *King Léopold III 168* (MO); 0-4 mi up Río Sabana from Santa Fe, *Duke 4159* (MO). PANAMA: Tocumen, *Dwyer 4350* (MO).

4. GOSSYPIUM L.

GOSSYPIUM L., Sp. Pl. 693. 1753, Gen. Pl. ed. 5, 309. 1754.

Herbs, shrubs or small trees, the stem and branchlets glabrous to densely pubescent, black-punctate with oil glands throughout. *Leaves* petiolate, the blade entire to usually 3- to 9-palmatilobed, the midvein and often also the principal, lateral veins bearing a dorsal gland (extrafloral nectary) near the base. *Flowers* axillary, solitary, pedicellate; epicalyx normally of 3 distinct or more or less united bractlets, these large, foliaceous, deeply incised-dentate and persistent, or very small, entire and caducous; calyx relatively small, cupuliform, truncate to 5-denticulate, persistent; petals 5, obovate, adnate to the base of the staminal tube, whitish, or yellow and often with a large, red or purple spot near the base, or purple, or red; staminal tube elongate but shorter than the corolla, the anthers very numerous, hippocrepiform; ovary 3- to 5-locular, the locules few- to many-ovulate; style unbranched and clavate, rarely divided at the tip, stigmatose apically. *Capsules* ovoid to subglobose, loculicidally dehiscent, the pericarp chartaceous to coriaceous, becoming dry and brittle; seeds numerous, commonly obovoid, often angulate, covered with lint (long, unicellular hairs) or with fuzz (a shorter indumentum) or with both, rarely nearly glabrous, exalbuminous; cotyledons plicate, black-punctate.

To this genus belong the cultivated cotton plants. Many species have been described, but these, for the most part, probably represent only individual variations, often resulting from interspecific hybridization. There are a few, truly wild, indigenous species in the warmer parts of North and South America, but none reported from Panama.

1. GOSSYPIUM BARBADENSE L., Sp. Pl. 693. 1753.—Fig. 3.

G. hirsutum sensu Mauer var. *panamicum* Mauer, Trudy po Prikl. Bot. Gen. Selek., Prilozh. **47**: 460, 553. 1930 (Bull. Appl. Bot. Gen. Pl.-Br., Suppl. **47**).
G. mexicanum sensu Standley, Contr. Arnold Arb. **5**: 101. 1933, non Todaro (1863).

Suffrutex, annual, or shrub, perennial, 1-4 m tall, the branches usually glabrescent to sometimes densely grayish-pubescent. *Leaves* long-petiolate, the stipules early or tardily caducous, the blade cordate at the base, usually deeply 3-lobed and often with 1 or 2 shorter, basal lobes, the lobes deltoid-ovate, with the sinuses often plicate and long-acuminate at the apex, entire-margined, usually 5(-7)-palminerved, mostly glabrescent to sometimes densely grayish-pubescent when young. *Flowers* large, the epicalyx of 3 bractlets, these usually shorter than the corolla, almost as long as broad, cordate at the base, laciniate with few, long, lance-subulate teeth at the apex, persistent; calyx truncate or shallowly 5-denticulate; corolla 3.5-5.5 cm long, pale yellow, turning pink or red; staminal tube about half as long as the corolla, filamentiferous nearly throughout, the filaments all of about the same length. *Capsule* ovoid, caudate-acuminate, normally 3-locular, usually 3-6

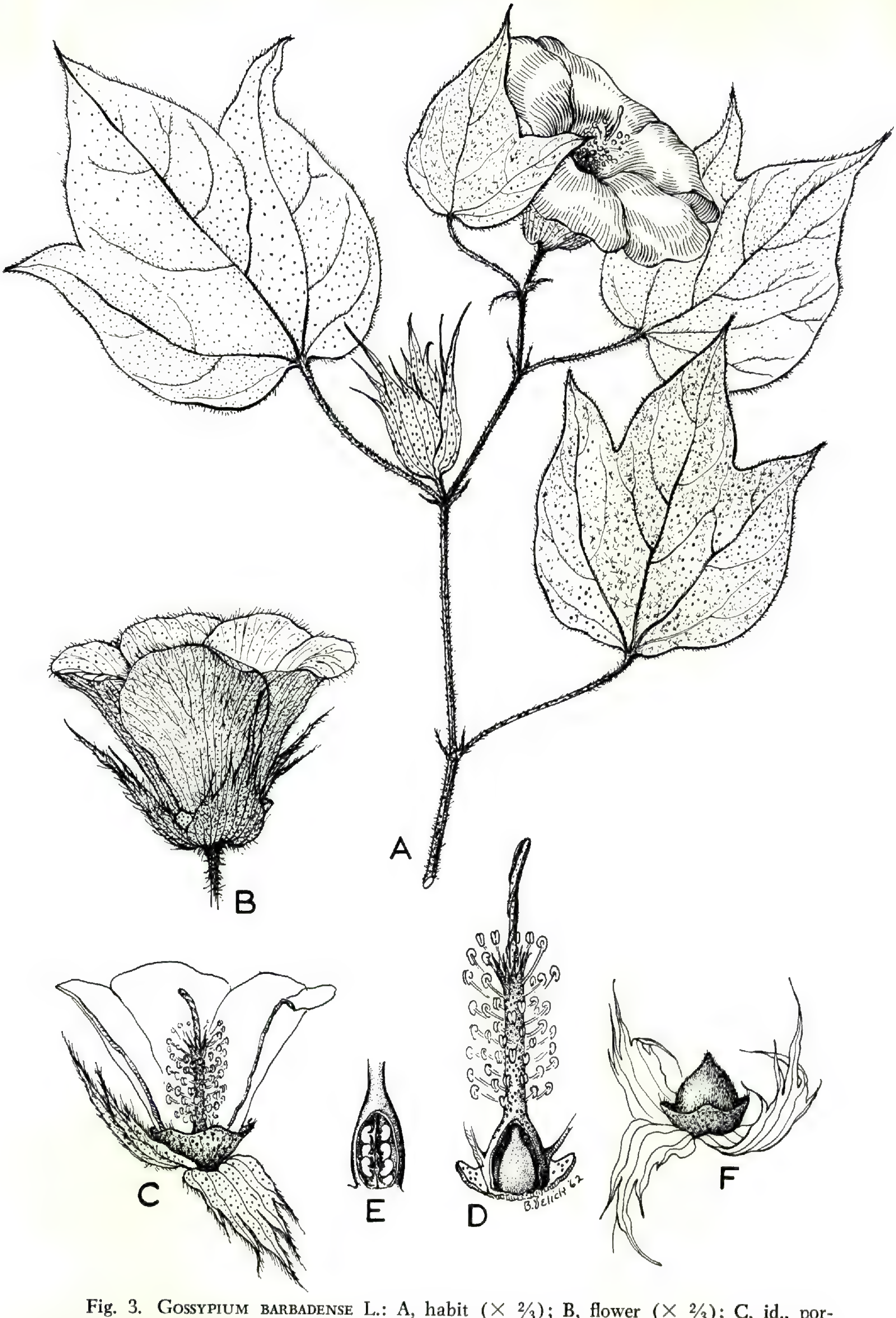

Fig. 3. GOSSYPIUM BARBADENSE L.: A, habit (× ⅔); B, flower (× ⅔); C, id., portion of corolla removed (× ⅔); D, androecium and pistil (× 1⅓); E, ovary, longitudinal section (× 2); F, young fruit (× ⅔). A-E after *Hunter & Allen 673;* F after *Allen 1091.*

cm long, the surface coarsely pitted, with black, oil glands in the pits; seeds free, with a copious and even coat of lint, with or without a coat of fuzz, sometimes fuzzy at one or both ends.

CANAL ZONE: vic of Fort Sherman, sandy thicket, *Standley 31219* (US); Barro Colorado Island, nr steps at beginning of Lutz Trail, *Woodworth & Vestal s.n.* (F); Frijoles, *Cooke & Martin 43* (US), *62* (US); Chagres arm of Gatun Lake, at junction of Río Aguardiente and Río Quebrada, plantation, *Maxon 6563* (US), *6564* (US); around Culebra, alt 50-150, *Pittier 4825* (US); in Government forest along Las Cruces Trail, alt 75 m, *Hunter & Allen 673* (MO); Pedro Miguel, wild, *Piper 5471* (US); Balboa, old field, *Standley 25643* (US). CHIRIQUÍ: Isla Parida, *Pittier 2816* (US). COCLÉ: Aguadulce, along the outskirts of the tidal belt, *Pittier 4971* (US). HERRERA: vic of Chitré, alt ca 20 m, *Allen 1091* (MO, US); vic of Ocú, alt 100 m, *Allen 4081* (MO). PANAMA: Bella Vista, nr strand at edge of woods, *Maxon & Valentine 6940* (US), coastal thicket, *Standley 25331* (US); between Matías Hernández and Juan Díaz, roadside, *Standley 31965* (US); Juan Díaz, roadside, *Standley 30537* (US); Isla Taboguilla, *Duke 5880* (MO).

Some of these collections were referred previously to *G. mexicanum* Todaro, which, according to Standley (Contr. U. S. Nat. Herb. **27:** 256. 1928), "is a frequent shrub about the zone, in thickets and along roadsides." *Gossypium mexicanum* was relegated to synonymy under *G. hirsutum* L. (Upland cotton) by Hutchinson (in Hutchinson *et al.*, The evolution of *Gossypium*, p. 40. 1947). The Panamanian specimens cited above resemble, however, *G. barbadense*, the species to which the Sea Island and Egyptian cottons belong, rather than *G. hirsutum.* Many of them were identified by Prokhanov as *G. tridens* Cook & Hubbard (which is a synonym of *G. nicaraguense* Ramirez Goyena, cf. Prokhanov, J. Bot. U. R. S. S. **32:** 75. 1947), the type of which was collected at Buenaventura, Colombia. It is doubtful that *G. tridens* is more than a form of *G. barbadense* with a more reduced epicalyx and capsule.

5. THESPESIA Solander ex Correa

THESPESIA Solander ex Correa, Ann. Mus. Hist. Nat. Paris **9:** 290. 1807, nom. gen. conserv.

Bupariti Duhamel, Sem. Plantat., Add. 5. 1760.

Shrubs or small trees, glabrous or lepidote or stellate-pubescent. *Leaves* long-petiolate, the stipules early caducous, the blade entire to 3- to 5-lobed. *Flowers* axillary, solitary, or forming terminal racemes or panicles by reduction of the upper leaves; epicalyx of 3-5 distinct, ovate to filiform bractlets, these persistent or early caducous; calyx cupuliform, usually truncate and 5-denticulate, persistent; corolla large, campanulate, the petals 5, adnate to the base of the staminal tube; staminal tube dentate or lobulate at the apex, filamentiferous on most of its length, the filaments short, the anthers hippocrepiform; ovary 5-locular, the locules 3- or 4-ovulate; style unbranched, clavate, bearing 5 stigmas. *Capsules* ligneous or leathery, indehiscent or tardily dehiscent; seeds few in each locule, obovoid or turbinate, glabrous or pubescent; cotyledons black-punctate.

A small, mainly Old World genus, although *T. populnea* (L.) Solander ex Correa is considered by some authors to be indigenous in America. *Thespesia* was reviewed by Hutchinson (New Phytol. **46:** 134-138. 1947), who included several

small genera that other authors (cf. Howard, Bull. Torrey Bot. Club **76:** 89-100, *fig. 1-14.* 1949) consider to be distinct.

Only one species is reported from Panama.

1. THESPESIA POPULNEA (L.) Solander ex Correa, Ann. Mus. Hist. Nat. Paris **9:** 290, *pl. 25 (1).* 1807.

Hibiscus populneus L., Sp. Pl. 694. 1753.
Malvaviscus populneus (L.) Gaertn., Fruct. Sem. **2:** 253, *pl. 135*(3). 1791.

Shrub or small tree up to 7 m tall, the branchlets densely lepidote especially when young. *Leaves* with petioles 4-12 cm long, lepidote, the stipules narrowly ovate to filiform, 5-7 mm long; blade broadly ovate, cordate at the base, acute to long-acuminate at the apex, entire-margined, up to 14(20) cm long and 12 cm broad, leathery, 5- to 7-palminerved, sparsely lepidote to glabrescent on both sides, the main veins prominent beneath. *Flowers* with the pedicel terete, inarticulated (or obscurely articulated?), 1.5-3.5 cm long, lepidote; epicalyx bractlets usually 3, subulate, ca 10-12 mm long and 2 mm broad, lepidote, early caducous; calyx truncate or shortly 5-denticulate, ca 8-10 mm high and 15 mm in diam, densely lepidote, more or less expanded in fruit; petals obovate, ca 5 cm long and 3.5 cm broad, yellow with a darker base, fading purple; staminal tube ca 3 cm long, 5-lobulate at the apex, the lobes ca 2 mm long, filamentiferous on the upper ⅔, the filaments 2-7 mm long, the anthers inequilaterally hippocrepiform; style exceeding the staminal tube, ca 3 cm long. *Capsule* depressed-globose, 1.5-2 cm high and 2-4.5 cm in diam, leathery, lepidote, indehiscent; seeds trigonous-obovoid, compressed, ca 1 cm long, more or less densely tomentellous.

Pantropical; generally along sea-shores; cultivated as a shade tree in Panama.

CANAL ZONE: Hospital Grounds at Ancon, alt 20-80 m, *Pittier 2745* (US); Balboa, planted, *Standley 30820* (F, US). COLÓN: Colón, in park, *Rose 22044* (US).

6. MALVAVISCUS Adans.

MALVAVISCUS Adans., Fam. Pl. **2:** 399. 1763.

Shrubs or small trees, sometimes vine-like in habit, the indumentum commonly of stellate hairs. *Leaves* petiolate, the stipules caducous, the blade entire to variously lobed. *Flowers* solitary in the axils or sometimes clustered at the apex of the branches, the pedicels short to elongate; epicalyx of 6-16 linear, lanceolate or spatulate bractlets; calyx campanulate, usually 5-lobed, variously pubescent; corolla funnelform, the 5 asymmetrically obovate-cuneate petals twisted, short-unguiculate, auriculate on one side at the base; staminal tube slender, usually long-exserted, 5-lobed at the apex, the anthers clustered below the apex; ovary 5-carpellate, each carpel 1-ovulate; style branches 10, the stigmas capitate. *Fruits* with an outer fleshy envelope, becoming dry, the 5 carpels usually separating at full maturity, stony, indehiscent, 1-seeded.

A small American genus, monographed by Schery in 1942 (Ann. Missouri Bot. Gard. **29:** 183-236). Only one species is at present known from Panama.

1. Malvaviscus arboreus Cav., Mon. Cl. Diss. Dec. 131, *t. 48(1)*. 1787.

Shrub or small tree up to 10 m but usually not more than 4 m high, sometimes clambering over other vegetation, very variable in indumentum, in shape of leaves and in size of flower parts, the branchlets velvety-pubescent to glabrescent. *Leaves* short- to usually long-petiolate, the petiole to 18 cm long; blade lanceolate to broadly ovate, or oblong-ovate, or slightly obovate, or slightly depressed ovate, entire to shallowly lobed, rounded, truncate or cordate at the base, commonly more or less acuminate at the apex, sinuate or crenulate to rather coarsely serrate to dentate at the margin, up to 21 cm long and 16 cm broad, thin, 5- to 7(-9)-palminerved, often scabridulous and usually with spreading, stellate hairs on both surfaces, the venation reticulate and slightly prominent on both sides. *Flowers* with the pedicel 1-6 cm long, glabrous to tomentellous; epicalyx equalling more or less the calyx, 11-20 mm long, the bractlets linear, narrowly lanceolate or sometimes more or less narrowly spatulate, glabrous to tomentellous; calyx 10-18 mm long, usually more or less deeply lobed, glabrous to tomentellous; petals obovate or sometimes narrowly obovate, emarginate or infrequently deeply lobed at the apex, 23-55 mm long and (7-)12-25 mm broad, deep pink to bright red; staminal tube 3-6 cm long. *Fruit* depressed-obovoid, ca 6-10 mm high and 8-13 mm in diam.

Southernmost United States and West Indies to Peru and Brazil; sea coast to elevations of 2000 m, in various habitats; often cultivated as an ornamental; known in Panama as *mapola* and *papito de monte.*

The species is represented in Panama by two varieties:

a. Petals obovate, emarginate at the apex, 23-55 mm long and 12-25 mm broad .... var. mexicanus

aa. Petals narrowly obovate, deeply lobate at the apex, ca 37 mm long and 7 mm broad, the lobes unequal, undulate, ca. 3.5-5 mm long .... var. lobatus

1a. Malvaviscus arboreus var. mexicanus Schlecht., Linnaea **11:** 359. 1837; Schery, Ann. Missouri Bot. Gard. **29:** 219, *fig.* 1942.—Fig. 4 (A-E).

M. penduliflorus Moç. & Sesse ex DC., Prodr. **1:** 445. 1824.
M. arboreus var. *penduliflorus* (Moç. & Sesse ex DC.) Schery, loc. cit. 223, *fig.*

bocas del toro: Almirante, *Cooper & Slater 26* (US), *Cooper 103* (F); Changuinola River, *Dunlap 101* (F), *349* (F, US), *440* (F); Water Valley, *von Wedel 657* (MO, US); Fish Creek Mountains, *von Wedel 2299* (MO, US); nr Chiriquí Lagoon, *von Wedel 1104* (MO), *1295* (MO); s. loc., *Carleton 81* (US). canal zone: Casa Larga trail, forest along telephone trail between the Río Indio Hydrographic Station and the Natural Bridge of Río Puente, *Dodge & Allen 17483* (MO). chiriquí: vic of New Switzerland, central valley of Río Chiriquí Viejo, alt 1800-2000 m, *Allen 1364* (F, MO, US); vic of Cerro Punta, 1500-2000 m, *Seibert 263* (MO); vic of Callejón Seco, Volcán de Chiriquí, alt 1700 m, *Woodson & Schery 506* (MO), *507* (MO); Bajo Chorro, elev 6000 ft, *Davidson 68* (F, MO); vic of Bajo Mona and Quebrada Chiquero, alt 1500 m, *Woodson & Schery 531* (MO), *550* (MO); Quebrada Velo, alt 1800 m, *Woodson & Schery 276* (MO); Cerro Horqueta, cloud forest, alt 6500 ft, *C. & W. von Hagen 2173* (NY); around El Boquete, alt 900-1500 m, *Dwyer 6968* (MO), *Bro. Maurice 690* (US), *Maxon 5000* (US), *Pittier 2925* (US), *3138* (US); Palo Alto, just E of Boquete, elev 5000 ft, *Stern et al. 1027* (MO); vic of San Bartolomé, Peninsula de Burica, alt 0-50 m, *Woodson & Schery 932* (MO); Finca Lérida to Peña Blanca, alt 1750-2000 m, *Woodson & Schery 302* (MO); vic of San Felix, alt 0-120 m, *Pittier 5210* (US). coclé: El Valle, *Dwyer 1834* (F); vic of El Valle, alt 600-1000 m, *Allen 91* (MO), *1176* (F, MO), *G. & P. White 70* (MO); N rim of El Valle, *Allen 1906*

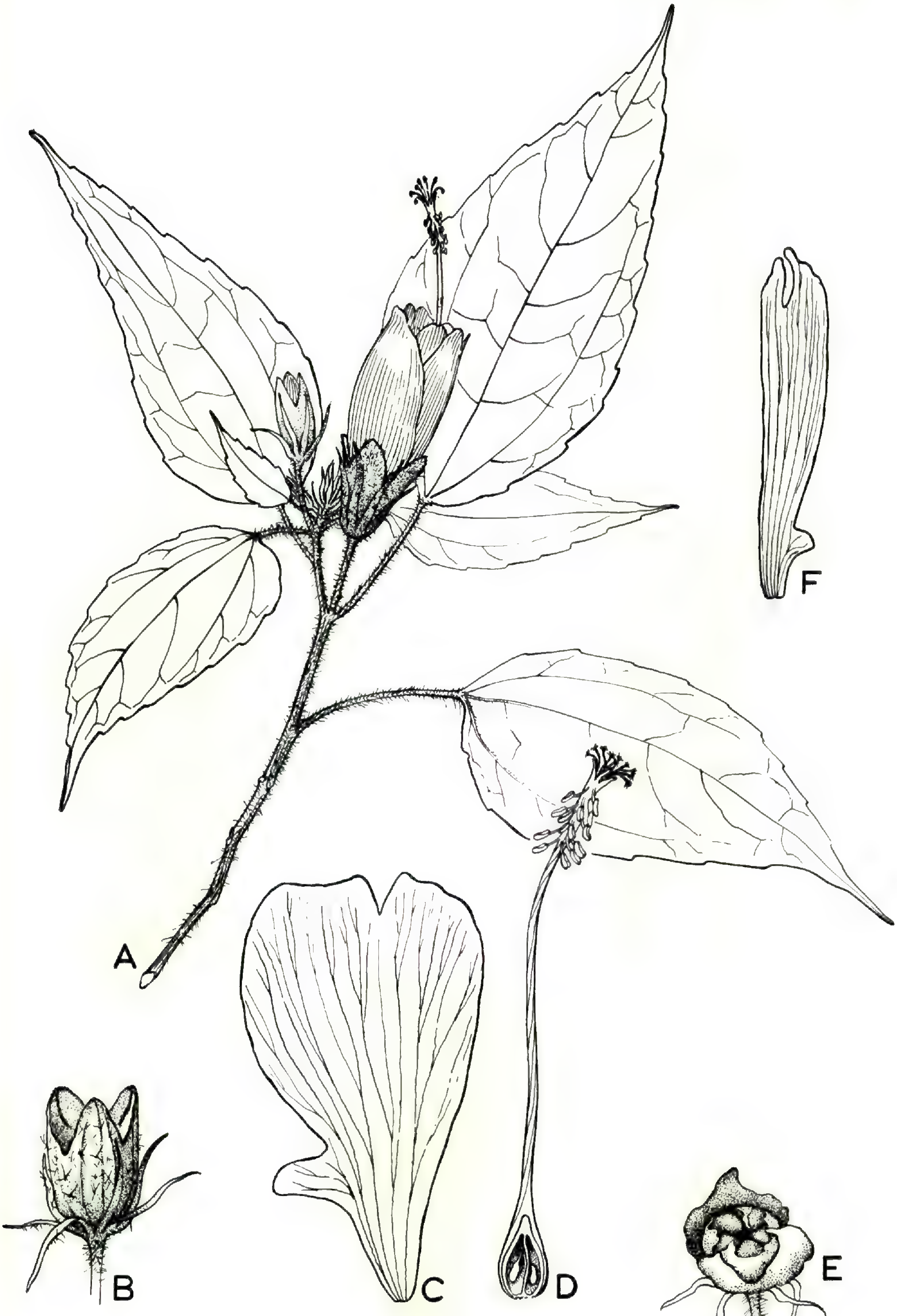

Fig. 4. MALVAVISCUS ARBOREUS Cav. var. MEXICANUS Schlecht.: A, habit (ca × ⅔); B, epicalyx and calyx (ca × 1⅓); C, petal (× 1⅓); D, androecium, longitudinal section of ovary, and stigmas (× 1⅓); E, fruit (× 1⅓); after *Allen 91*. M. ARBOREUS var. LOBATUS A. Robyns: F, petal (× 1⅓), after *Ebinger 692*.

(MO); N rim of El Valle de Antón, nr Cerro Turega, alt 650-700 m, *Woodson & Schery 188* (MO). DARIEN: Tucuti, *M. E. & R. A. Terry 1386* (F, MO). LOS SANTOS: Las Tablas, *Dwyer 2480* (MO). PANAMA: Río La Maestra, alt 0-25 m, *Allen 52* (MO); along road between Panama and Chepo, *Dodge et al. 16664* (MO); vic of El Llano, *Duke 5847* (MO); Taboga Island, *Standley 27924* (US). VERAGUAS: hills W of Soná, alt ca 500 m, *Allen 1045* (F, MO, US). PROVINCE UNKNOWN: *Stork 101* (US).

Schery, in his monograph (loc. cit. 205), recognized two varieties among the Panamanian collections cited above, the only distinction being the length of the petals (23-42 mm long in var. *mexicanus* and more than 42 mm in var. *penduliflorus*). As pointed out by Schery himself (p. 222), however, complete intergradation occurs between these two varieties and, consequently, I think that it is unnecessary to maintain this arbitrary disinction.

1b. MALVAVISCUS ARBOREUS var. **LOBATUS** A. Robyns, var. nov.—Fig. 4 (F).

Ab omnibus varietatibus petalis anguste obovatis apice profunde lobatis ca 37 mm longis et 7 mm latis lobisque inaequalibus undulatis et ca 3.5-5 mm longis sat recedit.

CHIRIQUÍ: Boquete, Fred Collins Finca, alt 6000 ft, edge of forest, *Ebinger 692* (holotype MO).

7. URENA L.

URENA L., Sp. Pl. 692. 1753, Gen. Pl. ed.5, 309. 1754.

Suffrutices, the indumentum usually of stellate hairs. *Leaves* petiolate, the stipules subulate and caducous; blade polymorphic, subentire to 3- to 5-palmatiparted, the 1 or 3 median veins on the dorsal surface bearing near the base an open, rounded or oblong gland (extrafloral nectary). *Flowers* axillary, solitary or in small glomerules, sometimes in terminal racemiform inflorescences, the pedicels short or the flowers subsessile; epicalyx of 5 partly united bractlets; calyx cupuliform, deeply 5-lobed, the lobes 1-nerved; petals 5, pink or purple; staminal tube about as long as the corolla, enlarged at the base, truncate at the apex, the anthers on short filaments, clustered subapically; ovary of 5 1-ovulate carpels; style branches 10, the stigmas discoid, fimbriate. *Fruits* separating into 5 indehiscent mericarps, these trigonous-obovoid, coriaceous, the dorsum convex and densely glochidiate-echinate; seeds trigonous-reniform, glabrous.

A pantropical, monotypic genus; the only species, *U. lobata* L., is extremely variable especially in shape of leaf blades and in indumentum (cf. Gürke, Engl. Bot. Jahrb. **16:** 361-385. 1892, and Hochreutiner, Ann. Conserv. Jard. Bot. Genève **5:** 131-146. 1901).

1. URENA LOBATA L., Sp. Pl. 692. 1753.

Suffrutex up to ca 3 m tall, the stem and branchlets sparsely to densely tomentose. *Leaves* with the petiole terete, up to 4 cm long, gradually shorter toward the apex of the stem and branchlets, sparsely to densely tomentose, the stipules ca 2-3 mm long; blade subcircular to ovate to oblong, subentire to angulate to 3-5-palmatilobed or palmatiparted, cuneate or rounded or cordate at the base, the lobes

Fig. 5. Urena lobata L. var. sinuata (L.) Hochr.: A, habit (× ⅔); B, base of dorsal leaf surface with gland on midrib (× 1⅓); after *Allen 91*. U. lobata var. lobata: C, flower (× 2); D, id., longitudinal section (×2⅔); after *von Wedel 2913*.

entire to pinnatisect, with rounded or acute sinuses and acute to obtuse at the apex, the margins often irregularly serrate, up to 12 cm long and broad, discolor, soft to scabridulous, 3- to 9-palminerved, puberulus to tomentose on both surfaces but the indumentum usually denser beneath, the venation reticulate and slightly prominent beneath. *Flowers* with the pedicel ca 3-5 mm long, tomentose; epicalyx campanulate, 4-7 mm long, the lobes narrowly ovate, connate in the lower ⅓, acute at the apex, pubescent; calyx usually slightly shorter than the epicalyx, the lobes narrowly ovate and acute, pubescent; petals obliquely obovate, rounded or truncate at the apex, shortly unguiculate, 10-18 mm long, flabellate-veined, puberulus outside, the claw barbate; staminal tube generally sparsely and minutely pilose; style branches exceeding scarcely the staminal tube. *Fruit* ca 10 mm in diam, the mericarps rounded at the apex, puberulus, dorsally densely glochidiate-echinate; seeds ca 2-3 mm long.

Urena lobata, a weed of wet pastures, roadsides and moist thickets, is represented in Panama by two varieties, which can be distinguished as follows:

a. Leaf blades generally subentire to angulately lobed .... var. LOBATA
aa. Leaf blades deeply 3- to 5-palmatiparted, the sinuses of the segments broad and rounded .... var. SINUATA

1a. URENA LOBATA var. LOBATA.—Fig. 5 (C-D).

BOCAS DEL TORO: Almirante, *Rowlee & Stork 1003* (US); Water Valley, *von Wedel 1705* (MO, US); Old Bank Island, *von Wedel 1871* (MO, US), *2043* (MO, US); Johns Creek, *von Wedel 2756* (MO, US); vic of Chiriquí Lagoon, *von Wedel 1286* (MO), *1354* (MO), *2913* (MO, US). CANAL ZONE: nr Fort Randolph, *Standley 28690* (US); Fort Davis, *Bro. Heriberto 38* (US); Mount Hope Cemetery, *Standley 28831* (US); nr Gatun, *Standley 27245* (US); Frijoles, *Maxon 4692* (US), *Piper 5811* (F, US), *Pittier 6843* (US), *Standley 31488* (US); Darien Station, *Standley 31590* (US); around Gamboa, alt 20-100 m, *Pittier 4795* (F, US); Obispo, *Standley 31786* (US); Las Cascadas Plantation, nr Summit, *Standley 25756* (US), 29643 (US). COLÓN: between France Field, Canal Zone, and Catival, *Standley 30259* (US). PROVINCE UNKNOWN: Bahia Honda, *Elmore H14* (F, US).

1b. URENA LOBATA var. SINUATA (L.) Hochr., Ann. Conserv. Jard. Bot. Genève **5:** 141. 1901.—Fig. 5 (A-B).

U. sinuata L., Sp. Pl. 692. 1753.

Known in Panama as *cepa de caballo.*

CANAL ZONE: Juan Mina Plantation, Río Chagres, region above Gamboa, *Allen 4126* (MO); Empire to Mandinga, *Piper 5502* (US); Las Cruces Trail, alt 75 m, *Hunter & Allen 715* (MO), *Standley 29033* (US); Camino de Corozal, *Bro. Heriberto 273* (US); between Corozal and Ancon, alt 10-30 m, *Pittier 2208* (US). PANAMA: vic of Juan Franco Race Track, nr Panama City, *Standley 27758* (US); Las Sabanas, *Standley 25885* (US); Río Tapía, *Standley 28145* (US); nr the big swamp E of the Río Tocumen, *Standley 26526* (US); Agricultural Experiment Station at Matías Hernández, *Pittier 6890* (US); between Matías Hernández and Juan Díaz, *Standley 31998* (US); Juan Díaz, *Standley 30599* (US); between Panama City and Chepo, *Dodge et al. 16635* (MO).

8. MALACHRA L.

MALACHRA L., Mant. Pl. 13. 1767.

Herbs or shrubs, the indumentum frequently hispid. *Leaves* petiolate, the stipules 2 or 4, the blade undivided to angulate to frequently 3- or 5-palmatilobed

or -palmatiparted. *Flowers* in dense, axillary or terminal, subsessile or pedunculate, capituliform inflorescences, these subtended by large, foliaceous bracts, the bracts expanded or conduplicate, often pellucid-scarious in age at the base, sometimes reflexed at the apex; epicalyx wanting or the bractlets 9-12; calyx cupuliform, 5-lobed or 5-parted, usually accrescent, the lobes 3-nerved; petals 5, obovate-unguiculate, asymmetrical, rounded to subbilobate at the apex, adnate to the base of the staminal tube, variously colored; staminal tube shorter than the corolla, 5-dentate at the apex, antheriferous above the middle, the filaments 15-30, short, the anthers reniform; ovary of 5 1-ovulate carpels, the ovules ascending; style branches 10, the stigmas capitellate-hirtellous. *Mericarps* 5, separating from the central columella, trigonous-obovoid, obtuse at the apex, acute at the base, dorsally convex, coriaceous, reticulate-veined, glabrous or not, ventrally dehiscent; seeds obovoid-reniform, glabrous.

A genus of about eight species, monographed by Gürke in 1892 (Engl. Bot. Jahrb. **16:** 330-361). The species, with one possible exception, are believed to be of American origin, although several of them are now widely distributed in the Old World tropics as weeds of roadsides and waste ground. Two species occur in Panama.

a. Flowers in terminal heads; bracts expanded, obtuse or rounded at the base; epicalyx of 9-12 bractlets; calyx lobes acute; petals pink; leaf blades usually deeply (often nearly to the base) 3- or 5-palmatiparted ....1. M. RADIATA

aa. Flowers in axillary heads; bracts conduplicate, subcordate to deeply cordate at the base; epicalyx wanting; calyx lobes long-aristate; petals yellow or white; leaf blades undivided to angulate to deeply 3- or 5-lobed ....2. M. ALCEIFOLIA

1. MALACHRA RADIATA (L.) L., Syst. Nat. ed. 12, 459. 1767.

Sida radiata L., Sp. Pl. ed. 2, 965. 1763.

Herb or suffrutex 0.5-2.5 m tall, the stem erect, terete and branched, the indumentum of stem, branchlets and petioles conspicuously hispid with long, mostly simple, flavescent hairs, and also with scattered, short, stellate hairs. *Leaves* rather long-petiolate, the petiole terete, 2-9 cm long, the stipules subulate-filiform, arcuate-erect, ca 1 cm long, hispid; blade usually deeply (often nearly to the base) 3- or 5-palmatiparted, cordate or subcordate at the base, the segments narrowly oblong, often lobed or laciniate, with rounded sinuses and subacute at the apex, the margins serrate, up to 12 cm long and broad, gradually smaller toward the apex of the stem and branchlets, 3- or 5-palminerved, scabrous and appressed-hispid with simple and few-forked, stellate hairs on both sides, or glabrescent above, the venation slightly prominent beneath. *Flowers* in terminal heads; bracts shortly petiolate (outer ones) to almost sessile (inner ones), oblong-ovate or lanceolate, infrequently sublobate, expanded, obtuse or rounded at the base, acuminate at the apex, irregularly and coarsely serrate-dentate, the outer ones up to 4 cm long and 3 cm broad, 5- or 7-palminerved, hispid with simple or few-forked, stellate hairs on both sides, the main veins prominulous beneath; epicalyx of 9-12 bractlets, these subulate-filiform, 10-12 mm long, hispid; calyx herbaceous, lobed to about the middle, 8-10 mm long, hispid, accrescent, the lobes lanceolate-ovate and acute;

petals 11-13 m long, pink; staminal tube 8-10 mm long; styles 10-12 mm long. *Mericarps* ca 4 mm long and 2.5-3 mm broad, glabrous; seeds ca 3 mm long.

West Indies and Central America to northern Argentina; tropical Africa.

PANAMA: Agricultural Experiment Station at Matías Hernández, *Pittier 6721* (US).

2. Malachra alceifolia Jacq., Collect. **2:** 350. 1788.

Herb, infrequently shrub, the stem erect, 0.6-2.0 m high, the indumentum of stem, branchlets and petioles more or less densely hispid with long, simple or forked, usually flavescent, tuberculate-based hairs, and also with scattered, short, stellate hairs, the latter rather dense at the nodes. *Leaves* long-petiolate, the petiole however gradually shorter toward the apex of the stem and branchlets, 2-10(-20) cm long, terete, the stipules subulate-filiform, arcuate-erect, 1-3 cm long, hispid with tuberculate-based hairs; blade subcircular to ovate, sometimes (especially the lower leaves) 5-angulate or shallowly to deeply 3- or 5-lobed, cordate or truncate or obtuse at the base, serrate-dentate to coarsely dentate at the margin, 3-15 cm long and 3-12 cm broad, 3- or 5- or 7-palminerved, glabrous or stellate-puberulus or appressed-hispid with mostly simple hairs on both surfaces, the indumentum usually slightly denser on the lower surface, the veins prominent beneath. *Flowers* in axillary, subsessile or up to 10 cm long pedunculate heads; bracts sessile to short-petiolate, ovate to broadly triangular, conduplicate, subcordate to deeply cordate at the base, acute to long-acuminate and sometimes reflexed at the apex, dentate or entire at the margin, the outer up to 25 mm long, the basal portion in age pellucid-scarious, 3- to 7-palminerved, flavescent-hispid with pustular-based hairs on both sides, sometimes also with minute, stellate hairs along the veins, prominently reticulate-veined beneath; calyx membranous, whitish except the brownish veins and awns, 5-lobed to below the middle, 4-7(-8) mm long, accrescent, hispid and sometimes also with minute, stellate hairs, the lobes lanceolate, long-aristate; petals 10-15 mm long, yellow or white; staminal tube 5-10 mm long; styles 6-10 mm long. *Mericarps* 3-3.5 mm long and 2-2.5 mm broad, minutely puberulus or glabrous; seeds ca 2-2.5 mm long.

Malachra alceifolia is a neotropical species extremely variable especially in indumentum, in shape of leaf blades and bracts, and in length of stipules. In Panama two varieties can be easily recognized: var. *alceifolia* and var. *fasciata*. The latter variety was retained as a species in Gürke's monograph of the genus (Engl. Bot. Jahrb. **16:** 330-361. 1892) (for discussion of the variability in the genus *Malachra*, see also Hochreutiner, Ann. Conserv. Jard. Bot. Genève **20:** 144-149. 1917).

Malachra alceifolia grows in moist thickets and weedy fields, among bushes, and on open slopes; the stiff hairs of stem and branchlets easily penetrate the skin; the var. *alceifolia* is called colloquially *malva*, while the var. *fasciata* is known in Panama as *malva macho* or *borraja*.

a. Stipules usually 1-1.5 cm long, infrequently up to 2 cm long; leaf blades entire, angulate or shallowly lobed, glabrous or stellate-puberulus; flower bracts broadly triangular, deeply cordate at the base, acute and usually not reflexed at the

apex; calyx 6-7(-8) mm long; petals ca 15 mm long, yellow; staminal tube 8-10 mm long; styles ca 10 mm long ....var. ALCEIFOLIA

aa. Stipules usually 2-3 cm long; leaf blades often (at least of the lower leaves) deeply lobed, appressed-hispid with mostly simple hairs; flower bracts ovate to broadly triangular, subcordate at the base, long-acuminate and mostly somewhat reflexed at the apex; calyx 4-5 mm long; petals ca 10 mm long, white or seldom yellow; staminal tube 5-6 mm long; styles ca 6-7 mm long ....var. FASCIATA

2a. MALACHRA ALCEIFOLIA var. ALCEIFOLIA.

Urena capitata (L.) Gomez de la Maza var. *alceifolia* (Jacq.) Gomez de la Maza, Anal. Soc. Esp. Hist. Nat. (Madrid) **19:** 219. 1890.

BOCAS DEL TORO: Water Valley, vic of Chiriquí Lagoon, *von Wedel 1775* (MO, US), *1843* (MO, US); Isla Colón, *von Wedel 56* (MO). CANAL ZONE: hills W of the Canal, nr Gatun, *Standley 27237* (US); Obispo, *Standley 31654* (US); Summit, *Standley 26929* (US); Juan Mina, *Piper 5686* (US); around Culebra, alt. 50-100 m, *Pittier 2159* (US); along the Las Cruces Trail, *Hunter & Allen 685* (MO), *747* (F, MO), *Standley 29167* (US); between Corozal and Ancon, alt. 10-30 m, *Pittier 2637* (US); Balboa, *Bro. Gervasius 12* (US), *13* (US), *Macbride & Featherstone 27* (F, US), *Standley 25557* (US), *30883* (US). DARIEN: edge of road on Don Pablo Othon's farm, vic of El Real, Río Tuira, *Stern et al. 802* (MO, US); along Río Pirre, *Duke 4973* (MO). HERRERA: vic of Chitré, alt ca 20 m, *Allen 1095* (F, MO, US). PANAMA: Las Sabanas, *Bro. Heriberto 298* (US); Bella Vista, *Standley 25334* (US); Agricultural Experiment Station at Matías Hernández, *Pittier 6887* (US); between Matías Hernández and Juan Díaz, *Standley 31972* (US); banks of Mamoni River, above La Capitano, alt 20-25 m, *Pittier 4737* (US); Taboga Island, *Allen 1298* (F, MO, US), *Standley 27113* (US); San José Island, *Johnston 873* (GH, MO).

2b. MALACHRA ALCEIFOLIA var. **FASCIATA** (Jacq.) A. Robyns, stat. nov.

M. fasciata Jacq., Collect. **2:** 352. 1788.

CANAL ZONE: Chagres, Isthmus of Panama, *Fendler 23* (MO, US); nr Fort Randolph, *Standley 28755* (US); Darien Station, *Standley 31585* (US); Gamboa, *Standley 28324* (US); Empire to Mandinga, *Piper 5447* (US), *5464* (US); Las Cascadas Plantation, nr Summit, *Standley 29626* (US); Summit, *Standley 26909* (US); Río Grande, nr Culebra, alt 50-100 m, *Pittier 2135* (US); around Culebra, alt 50-150 m, *Pittier 4820* (US); along the old Las Cruces Trail, between Fort Clayton and Corozal, *Standley 29040* (US); vic of Miraflores Lake, *P. White 264* (F, MO); Albrook, *Dwyer & A. Robyns 176* (MO); Balboa, *Bro. Gervasius 11* (US), *J. M. & M. T. Greenman 5039* (MO), *Standley 25530* (US), *25506* (US). PANAMA: along the Corozal Road, nr Panama, *Standley 26788* (US); Las Sabanas, *Bro. Celestine 106* (US), *Bro. Heriberto 292* (US); between Savanas and Río Yguana, *Macbride 2662* (F, US); vic of Juan Franco Race Track, nr Panama, *Standley 27692* (US); between Matías Hernández and Juan Díaz, *Standley 32005* (US); Tocumen Airport, *Dwyer 4094* (MO).

9. PAVONIA Cav.

PAVONIA Cav., Mon. Cl. Diss. Dec. (sub *Genera elucidanda* ad finem Diss. 2). 1786; 132. 1787, nom. gen. conserv.

Lass Adans., Fam. Pl. **2:** 400. 1763.
Malache Vogel in Trew, Pl. Select. 50. 1772.
Lopimia Mart., Nov. Acta Acad. Caes. Leop.-Carol. **11:** 96. 1823.
Malachra L. sect. *Peltaea* Presl, Rel. Haenk. **2:** 125. 1836.
Asterochlaena Garcke, Bot. Zeitung **8:** 666. 1850.
Peltaea (Presl) Standley, Contr. U. S. Nat. Herb. **18:** 113. 1916.

Herbs, undershrubs or shrubs, infrequently small trees, the indumentum

mostly of stellate hairs. *Leaves* usually petiolate, the blade simple to palmatiparted, palminerved. *Flowers* axillary and solitary or in corymbiform, racemiform or paniculiform, terminal inflorescences, generally pedicellate; epicalyx of 5 - ∞ bractlets, these distinct or more or less united at the base, sometimes adnate to the base of the calyx, persistent; calyx 5-merous, campanulate or cupuliform, dentate or lobate, rarely apiculate, persistent; petals erect or spreading, more or less unguiculate, adnate to the base of the staminal tube, longer than the calyx, variously colored; staminal tube shorter to longer than the corolla, antheriferous throughout or usually on the upper part only below the 5-dentate or 5-lobate apex, the filaments few to numerous, terete, the anthers reniform; ovary 5-locular, the locules 1-ovulate; style branches 10, the stigmas capitate or discoid. *Fruit* separating into 5 mericarps, these usually triquetrous-obovoid, muticous or awned, glabrous or not, more or less dehiscent; seeds glabrous or variously pubescent; endosperm absent; cotyledons folded.

A tropical and subtropical genus of over 200 species, distributed in both hemispheres but particularly well represented in South America; 15 species are known from Panama.

Useful references are:

Kearney, T. H., A tentative key to the North American species of *Pavonia* Cav. Leafl. West Bot. **7:** 122-130. 1954.

———, T. H., A tentative key to the South American species of *Pavonia* Cav. Leafl. West. Bot. **8:** 225-246. 1958.

a. Epicalyx bractlets linear, abruptly expanded at the apex into a more or less peltate, small blade; flowers subtended by large, foliaceous bracts; mericarps muticous or shortly mucronulate (sect. *Peltaea*).
  b. Leaf blades ovate to subcircular, infrequently shallowly lobed, 7- to 9-palminerved, densely stellate-puberulus to stellate-tomentellous or stellate-velutinous on both sides; mericarps glabrous .... 1. P. SESSILIFLORA
  bb. Leaf blades ovate to narrowly ovate, 3- to 5-palminerved, roughly stellate-puberulus on both sides; mericarps minutely puberulus .... 2. P. RIEDELII var. OVATA

aa. Epicalyx bractlets not expanded at apex; flowers not subtended by large, foliaceous bracts.
  c. Mericarps muticous or 3-crested or cuspidate (sect. *Eupavonia*).
    d. Mericarps muticous (sometimes short-mucronulate, cf. *P. paniculata*).
      e. Epicalyx bractlets 12-24; calyx 1/3 as long as the epicalyx or shorter; petals 2.1-5 cm long; mericarps with a mucilaginous coat, brown to blackish and more or less shiny when dry.
        f. Stipules ovate-subulate, 8-13 mm long; epicalyx bractlets 15-24, linear-subulate, 10-15 mm long and 0.6-1 mm wide, densely long-hispid; petals 2.1-3 cm long .... 3. P. MALACOPHYLLA
        ff. Stipules narrowly ovate, ca 20 mm long; epicalyx bractlets 12-16, narrowly ovate, (12-)18-28 mm long and (1-)2-3 mm wide, densely stellate-puberulus to stellate-velutinous; petals 3-5 cm long .... 4. P. DASYPETALA
      ee. Epicalyx bractlets 5-13; calyx 1/2 to sometimes nearly as long as the epicalyx; petals 0.4-2.5 cm long; mericarps not mucilaginous-coated.
        g. Epicalyx bractlets linear to linear-filiform, acute, 4-10 mm long and 0.5-0.8 mm wide; petals 4-15 mm long, white or yellow.

h. Flowers solitary in the upper leaf axils; petals white, 4-8 mm long; mericarps with an inconspicuous, longitudinal rib dorsally, otherwise nearly smooth; epicalyx bractlets 6-8, 4-8 mm long; glandular hairs absent ....5. P. ALBA

hh. Flowers solitary in the upper leaf axils, usually forming paniculiform inflorescences by reduction of the uppermost leaves, or the flowers subcorymbosely clustered at the end of the branchlets; petals yellow, 10-15 mm long; mericarps foveolate-rugose dorsally; epicalyx bractlets 6-12, 7-10 mm long; indumentum with glandular hairs ....6. P. PANICULATA

gg. Epicalyx bractlets 6-9, narrowly ovate, short-unguiculate, long-acuminate, 10-20 mm long and 2.5-5 mm wide; petals 18-25 mm long, yellow, reddish at the base ....7. P. SIDIFOLIA

dd. Mericarps 3-crested or cuspidate.

i. Leaf blades ovate to broadly ovate, cordate at the base, 5(-7)-palminerved; mericarps with 3 broad, apical crests ....8. P. SPICATA

ii. Leaf blades narrowly ovate or narrowly oblong-ovate, rounded to subcordate at the base, 3- to 5-palminerved; mericarps with a single, stout, triangular, apical and proximal cusp ca 3 mm long, sometimes also with 2 prominulous, apical and distal crests ......9. P. RHIZOPHORAE

cc. Mericarps 3-aristate, the awns retrorsely hispidulous or setose (sect. *Typhalaea*).

j. Awns proximate at the apex; epicalyx bractlets 5-6, these united for less than $\frac{1}{4}$ of their length; flowers in small, dense, corymbiform or subcapitate inflorescences ....10. P. FRUTICOSA

jj. Awns apical but not proximate or the central awn apical and the marginal lower down.

k. Petals 20-40 mm long, yellow; flowers solitary or somewhat clustered; epicalyx of 5-8 nearly distinct bractlets; mericarps with the central awn apical and the marginal markedly below ....11. P. SPINIFEX

kk. Petals 7-16 mm long.

l. Epicalyx bractlets 11-13, ca 5-6 times longer than the calyx, distinct, 15-20 mm long; flowers solitary, long-pedicellate; petals 10-12 mm long; mericarps with the awns apical but not proximate ....12. P. OXYPHYLLARIA

ll. Epicalyx bractlets 7-11, at maximum 3 times longer than, equalling more or less, or slightly shorter than the calyx.

m. Leaf blades asymmetrical, oblique at the base; flowers solitary, pendulous, long-pedicellate; epicalyx bractlets 8-10, slightly shorter than to equalling the calyx, nearly distinct, 5.5-7 mm long; calyx 6.5-8 mm long; petals 14-16 mm long; mericarps broadly trigonous-obovoid, ca 8 mm long and 5.5 mm wide, the central awn apical, the marginal markedly below the apex ....13. P. PENDULIFLORA

mm. Leaf blades symmetrical; flowers in few-flowered fascicles; epicalyx bractlets longer than the calyx.

n. Epicalyx bractlets 8-10, united for ca $\frac{1}{3}$-$\frac{1}{2}$ of their length, 6-8.5 mm long; calyx 3 mm long; petals ca 7 mm long; mericarps narrowly trigonous, 6-8 mm long and 2-2.3 mm wide, the awns apical but not proximate ....14. P. LONGIPES

nn. Epicalyx bractlets 7-11, united for maximum $\frac{1}{4}$ of their length, 5.5-11 mm long; calyx 3-5 mm long; petals 8-13 mm long; mericarps trigonous-obovoid, 5-7 mm long and ca 2.5-3.5 mm wide, the central awn apical, the marginal below the apex ....15. P. ROSEA

1. PAVONIA SESSILIFLORA H. B. K., Nov. Gen. Sp. Pl. **5:** 281. 1822.

P. involucrata Klotzsch, Linnaea **14:** 301. 1840.
P. bracteosa Benth., Hook. J. Bot. **4:** 118. 1842.
Peltaea sessiliflora (H. B. K.) Standley, Contr. U. S. Nat. Herb. **18:** 113. 1916.

Herb or shrub 0.6-2.4 m high, the stem erect, sparingly branched, densely stellate-puberulus to stellate-tomentellous. *Leaves* rather short-petiolate, the petiole 5-20 mm long, densely stellate-puberulus to stellate-tomentellous, the stipules subulate-filiform; blade ovate to subcircular, infrequently shallowly lobed, cordate at the base, obtuse, acute or short-acuminate at the apex, irregularly crenate-dentate at the margin, up to 10 cm long and 7 cm wide, 7- to 9-palminerved, densely stellate-velutinous on both sides, the indumentum however always denser beneath, the nervation prominent and reticulate on the lower surface. *Flowers* solitary in the axils or in few-flowered clusters at the ends of small accessory branchlets, sessile or the pedicel very short and stout, the bracts large and foliaceous; epicalyx of 9-11 bractlets, these linear, abruptly expanded at the apex into a more or less peltate, small blade, 5-10 mm long, hirsute; calyx cupulate, deeply lobed, shorter to longer than the epicalyx, hirsute, the lobes ovate-lanceolate, acute or subacuminate; petals broadly cuneate-obovate, shortly unguiculate, rounded at the apex, up to 22 mm long, yellow; staminal tube shorter than to nearly equalling the corolla, antheriferous throughout or on the upper ⅔; style slightly longer than the staminal tube, the stigmas capitellate. *Mericarps* triquetrous-obovoid, shortly mucronulate, dorsally convex, 2.5-3 mm long, membranous, with a longitudinal dorsal rib, smooth and glabrous; seeds trigonous reniform, glabrous.

Trinidad and Costa Rica to Colombia, Brazil and Paraguay; thickets, wet savannas, grassy slopes and old fields, often growing in water; it is called *guacimillo* in Panama.

CANAL ZONE: Cerro de Ancon, *Bro. Celestine 79* (US), *Standley 25511* (US). COCLÉ: Aguadulce, nr sea level, *Pittier 4884* (US); Penonomé and vic, *R. S. Williams 144* (US). PANAMA: between Capira and Potrero, alt 80-130 m, *Dodge & Hunter 8638* (MO); Las Sabanas, *Bro. Heriberto 280* (US), *Pittier 6864* (US), *Standley 25851* (US); between Las Sabanas and Matías Hernández, *Standley 31809* (US); nr Matías Hernández, *Standley 28860* (US); W of Juan Díaz, *Killip 3264* (US); Río Tapía, *Standley 28107* (US); Tocumen, *Dwyer 4048* (MO); E of Río Tocumen, *Standley 26511* (US); along road between Panama and Chepo, *Dodge et al. 16704* (MO); Laguna de Portala, nr Chepo, alt 50 m, *Pittier 4638* (US); Taboga Island, *Standley 28023* (US).

2. PAVONIA RIEDELII Gürke in Mart., Fl. Bras. **12**(3): 493, *pl. 91*(2). 1892.

Herb or shrub up to 2.5 m high, the stem minutely and more or less roughly stellate-puberulus. *Leaves* rather short-petiole, the petiole up to 2.7 cm long, roughly stellate-puberulus, the stipules subulate-filiform; blade ovate to narrowly ovate, rounded to subcordate at the base, obtuse, acute or more or less acuminate at the apex, irregularly serrate-crenate at the margin, up to 8 cm long and 4.5 cm wide, 3- to 5-palminerved, the roughly stellate-puberulus indumentum denser on the lower surface, the venation prominent and reticulate beneath. *Flowers* as in *P. sessiliflora*. *Mericarps* triquetrous-obovoid, shortly mucronulate, dorsally convex, 3-3.5 mm long, membranous, with an inconspicuous, dorsal, longitudinal rib,

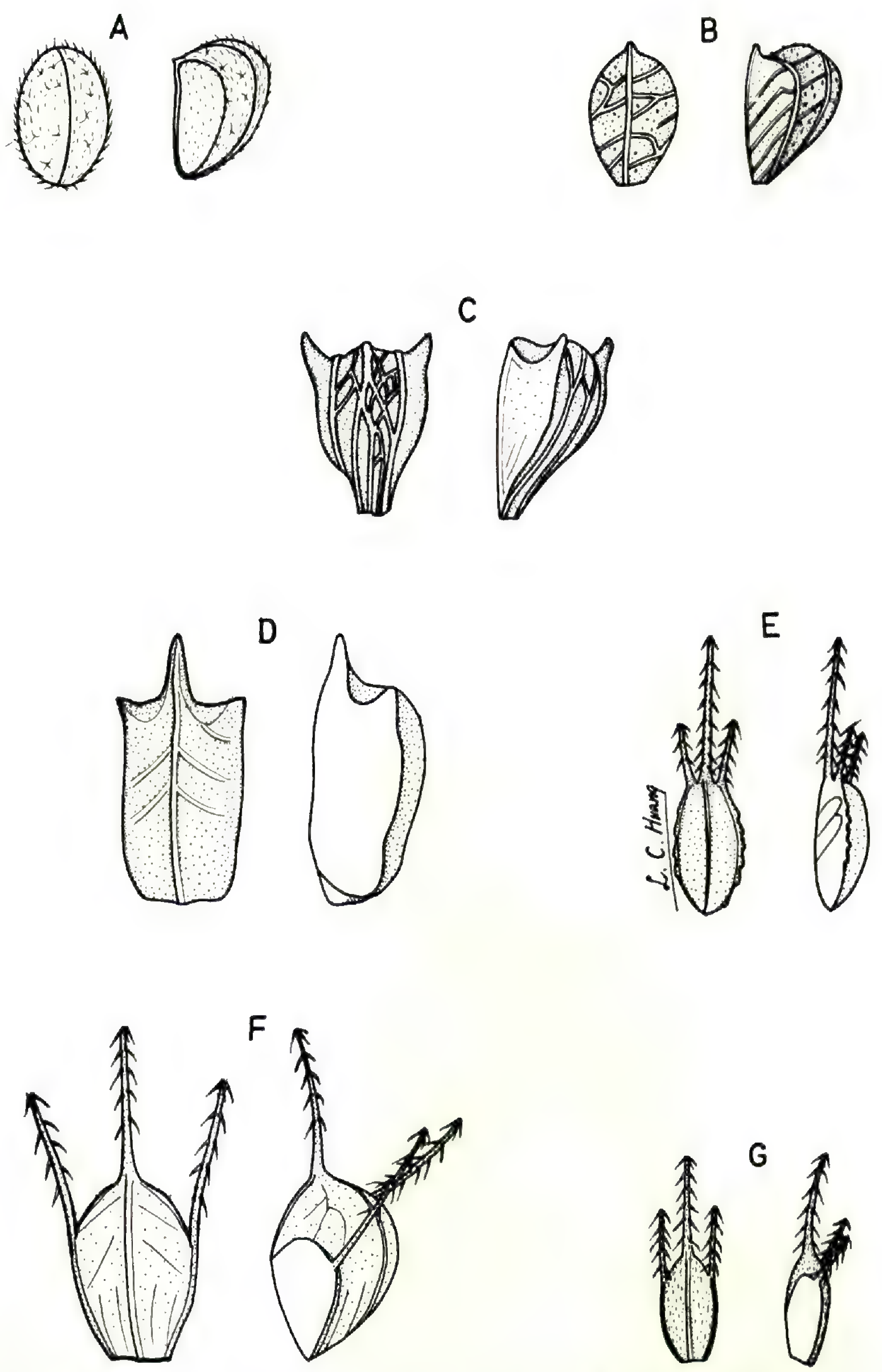

Fig. 6. PAVONIA RIEDELII Gürke var. OVATA (Presl) A. Robyns: A, mericarp, dorsal and lateral view (× 5), after *A. Robyns 65-48*. P. PANICULATA Cav.: B, id. (× 5), after *Dodge & Hunter 8646*. P. SPICATA Cav.: C, id. (× 2½), after *McDaniel 5159*. P. RHIZOPHORAE Killip: D, id. (× 2½), after *Dwyer 2286*. P. FRUTICOSA (Mill.) Fawcett & Rendle: E, id. (× 2½), after *Stern et al. 237*. P. PENDULIFLORA (Standley) Standley: F, id. (×2½), after *Bro. Maurice 877*. P. ROSEA Schlecht. var. ROSEA: G, id. (× 2½), after *Dwyer 2107*.

minutely puberulus with both simple and stellate hairs, very dehiscent; seeds trigonous-reniform, ca 2.5 mm long, glabrous.

The species is represented in Panama by the following variety:

Pavonia riedelii var. **ovata** (Presl) A. Robyns, stat. nov. et comb. nov.—Fig.6 (A).

Malachra ovata Presl, Rel. Haenk. **2**: 125. 1835, non *Pavonia ovata* Spreng. (in L., Syst. Veg. ed. 16: **3**: 99. 1826.)
Peltaea ovata (Presl) Standley, Contr. U. S. Nat. Herb. **18**: 113. 1916.
Pavonia preslii Standley, J. Wash. Acad. Sci. **17**: 168. 1927.

The var. *ovata* is distinguished by its usually ovate and 5-palminerved leaf blades, while the var. *riedelii* (Brazil, Peru, Bolivia) is characterized by its rather narrowly ovate and generally 3-palminerved leaf blades.

Panama, Colombia (?) and Venezuela; in water, among bushes and in brushy fields.

canal zone: Chagres, Isthmus of Panama, *Fendler 21*, (MO, US); Darien Station, *Standley 31584* (US); Navy Reservation, N of Gamboa, *A. Robyns 65-48* (MO); Empire to Mandinga, *Piper 5466* (US); Summit, *Standley 26949* (US); around Culebra, alt 50-150 m, *Pittier 2149* (US); vic of Miraflores Lake, *P. White 262* (F, MO); hills W of Curundu, *Harvey 5234* (F). panama: Las Sabanas, NE of Panama City, *Bro. Paul 213* (US). veraguas: hills W of Soná, alt ca 500 m, *Allen 1057* (F).

3. Pavonia malacophylla (Link & Otto) Garcke, Jahrb. K. Bot. Gart. Mus. Berlin **1**: 221. 1881.

Sida malacophylla Link & Otto, Ic. Pl. Selec. Hort. Reg. Bot. Berol. 67, *t. 30.* 1822.
Lopimia malacophylla (Link & Otto) Mart., Nova Acta Acad. Caes. Leop.-Carol. **11**: 97. 1823.
Pavonia velutina St.-Hil. *et al.*, Fl. Bras. Merid. **1**: 182. 1827.

Herb or shrub 1-4 m tall, the stem velutinous with short, viscid, stellate hairs. *Leaves* long-petiolate, the petiole up to 17 cm long, stellate-velutinous, the stipules ovate-subulate, 0.8-1.3 cm long; blade ovate to subcircular, sometimes subangulate, cordate at the base, acute at the apex, serrate-denticulate at the margin, 3-20 cm long and wide, 5- to 7-palminerved, the stellate-velutinous-tomentose indumentum denser on the lower surface, the venation prominent beneath. *Flowers* axillary, solitary or frequently clustered toward the apex of the branchlets and forming paniculate inflorescences, the pedicel 0.5-6 cm long, tomentose; epicalyx bractlets 15-24, distinct, linear-subulate, 10-15 mm long and 0.6-1 mm wide, densely long-hispid, explanate in fruit; calyx cupuliform, 3-6 mm long, thin, appressed-hirsute, the lobes deltoid, acute and ca 1-2.5 mm long, explanate in fruit; petals cuneate-obovate, shortly unguiculate, 2.1-3 cm long and 0.75-1.3 cm wide, red, pink or white (cf. exsiccatae from San José Island); staminal tube 1.9-2.5 cm long, lobulate, antheriferous on the upper ½, the filaments 3-5 mm long; style slightly longer than the staminal tube, the branches 2-4 mm long, the stigmas capitate. *Mericarps* trigonous-obovoid, obtuse and muticous at the apex, dorsally convex, 3-5 mm long and 2 mm wide, glutinous, brown to blackish and more or less shiny when dry, slightly reticulate-veined, glabrous; seeds 3-4 mm long, glabrous.

Southern Mexico to Brazil and Bolivia; Cuba.

canal zone: Ancon Hill, *Gillespie P-16* (US), *Piper 5557* (US). panama: banks of Río Utibe, N of Pacora, alt below 300 ft, *Bro. Maurice 793* (MO, US); San José Island, *Erlanson 56* (GH), *Johnston 552* (GH, US), *840* (GH).

According to Johnston (Sargentia **8:** 196. 1949), the herbage is "very clammy and unpleasant to handle" and the glutinous mericarps adhere to clothing. He describes the corolla as white, but this appears to be an exceptional phase.

4. PAVONIA DASYPETALA Turcz., Bull. Soc. Imp. Nat. Moscou **31**(1): 189. 1858.

Lopimia dasypetala (Turcz.) Standley, Contr. U. S. Nat. Herb. **18:** 114. 1916.

Suffrutex or shrub 1-5 m high, the stem stellate-pubescent to stellate-velutinous. *Leaves* long-petiolate, the petiole up to 15 cm long, stellate-puberulus to stellate-velutinous, the stipules narrowly ovate, long-acute, ca 20 mm long and 2-4 mm wide; blade broadly ovate, cordate at the base, acute to more or less acuminate at the apex, irregularly serrate-dentate at the margin, up to 23 cm long and 20 cm wide, 5- to 7-palminerved, stellate-puberulus to stellate-velutinous on both sides, the indumentum always denser on the lower surface, the nervation prominent beneath. *Flowers* axillary, solitary or usually clustered toward the apex of the branchlets and forming paniculate inflorescences, the pedicel articulated below the apex, up to 3.5 cm long, shortly stellate-velutinous; epicalyx bractlets 12-16, nearly distinct, narrowly ovate, long-acute, (12-)18-28 mm long and (1-)2-3 mm wide, densely stellate-puberulus to stellate-velutinous; calyx cupuliform, shortly 5-apiculate to broadly and shortly 5-dentate, ca (1-)2-4 mm long, thin, subglabrous to sparsely and minutely stellate-puberulus; petals narrowly obovate, 3-5 cm long and 1-1.2 cm wide, rose; staminal tube somewhat shorter than the corolla, lobulate, antheriferous on the upper part, the filaments ca 5-7 mm long; style longer than the staminal tube, the branches up to 7 mm long, the stigmas capitellate. *Mericarps* obovoid, more or less trigonous, obtuse and muticous at the apex, dorsally convex, ca 6 mm and 3 mm wide, with a mucilaginous coat, blackish, prominently reticulate-veined, glabrous; seeds 4-4.5 mm long, glabrous.

Costa Rica, Panama, Colombia and Venezuela; thickets and edges of forests, sometimes in wet soil.

CANAL ZONE: Lion Hill, Gatun, *Goldman 1855* (US); railroad relocation between Gorgona and Gatun, alt 10-15 m, *Pittier 2273* (US); along Río Chagres between junction with Río Pequení and with Río Indio, alt 66 m, *Steyermark & Allen 16778* (MO); along banks of Quebrada La Palma and Cañon of Río Chagres, alt 70-80 m. *Dodge & Allen 17333* (MO); Barro Colorado Island, *Aviles 30* (F), *Shattuck 505* (F, US), *Standley 31418* (US), *Wetmore & Abbe 52* (F), *106* (F), *Woodworth & Vestal 415* (F); hills N of Frijoles, *Standley 27499* (US). PANAMA: Panama City, *Hayes 216* (US).

5. PAVONIA ALBA Seem., Bot. Voy. Herald 81. 1853; Kearney, Leafl. West. Bot. **7:** 119. 1954.

Malache panamensis Standley, Contr. U. S. Nat. Herb. **18:** 116. 1916.
Pavonia panamensis (Standley) Standley, J. Wash. Acad. Sci. **17:** 168. 1927.

Herb or suffrutex up to 2 m high, the stem slender, cinereous-puberulus, the short, simple or stellate hairs sometimes intermixed with long, simple hairs. *Leaves* rather long-petiolate, the petiole slender, up to 4.5 cm long, puberulus to more or less shortly villous and sparsely long-hirsute, the stipules subulate; blade ovate to

lanceolate, rounded to cordate at the base, acute to acuminate at the apex, coarsely crenate-serrate at the margin, up to 8 cm long and 3.5 cm wide, 3(-5)-palminerved, sparsely puberulus and mostly with simple hairs above, more or less pubescent and with appressed stellate hairs beneath, the main veins slightly prominent beneath. *Flowers* solitary in the upper leaf axils, forming elongate, leafy, much-branched panicles, the pedicel elongate, very slender, articulated above the middle, up to 2-3.5 cm long, shortly villous and hirsute; epicalyx of 6-8 bractlets, these distinct, more or less linear, acute, 4-8 mm long and 0.5-0.8 mm wide, minutely puberulus and hirsute-ciliate; calyx lobed to about or to below the middle, usually about ½ as long as to sometimes nearly equalling the epicalyx, 3.5-5 mm long, hirsute, the lobes deltoid-ovate, acute; petals 4-8 mm long, white; staminal tube about ½ as long as the corolla, lobulate, antheriferous throughout; style slightly longer than the staminal tube. *Mericarps* triquetrous-obovoid, rounded and muticous at the apex, dorsally convex, ca 2.5 mm long, with an inconspicuous, longitudinal rib dorsally, otherwise nearly smooth and glabrous, very dehiscent; seeds reniform, ca 2 mm long, minutely puberulus.

Known only from Panama and Colombia; edges of forests and roadsides.

CANAL ZONE: along Las Cruces trail, alt 75 m, *Hunter & Allen 757* (MO); Cerro de Ancon, *Seemann 90* (type K, fide Kearney, loc. cit.); Sabana of Panama, alt 10-50 m, *Pittier 2548* (type of *M. panamensis*, US); along the Corozal road, nr Panama, *Standley 26846* (US). PANAMA: between Capira and Potrero, alt 80-130 m, *Dodge & Hunter 8643* (MO); Capira, alt 300 ft, *Bro Maurice 806* (US); Río Potrero, ca 2 mi from Arraíjan, *Duke 4677* (MO); Agricultural Experiment Station at Matías Hernández, *Pittier 6907* (US); Chepo, alt ca 60 m, *Pittier 4448* (US).

6. Pavonia paniculata Cav., Mon. Cl. Diss. Dec. 135, *t.* 46(2). 1787.—Fig. 6 (B).

Herb, suffrutex or shrub, 1-3 m high, the stem usually freely branched above, glandular-pilose and hirsute with long, simple or sometimes stellate hairs. *Leaves* rather long-petiolate, the petiole slender, up to 10 cm long, glandular-pilose and hirsute, the stipules narrowly ovate; blade ovate to broadly ovate, sometimes more or less deltoid or 3-lobed, truncate-subcordate to cordate at the base, acute to long-acuminate at the apex, crenate-serrate at the margin, up to 12 cm long and 10 cm wide, somewhat discolorous and scabrous, 7- to 9-palminerved, rather sparsely puberulus with stellate or simple hairs above, appressed-stellate-pubescent and with the main veins prominent beneath. *Flowers* numerous, solitary in the leaf axils, usually forming paniculiform inflorescences by reduction of the uppermost leaves, or the flowers subcorymbosely clustered at the end of the branchlets, the pedicel short or elongate, articulated above the middle, up to 3 cm long, glandular-pilose and hirsute; epicalyx of 6-12 bractlets, these distinct, linear-filiform, acute, 7-10 mm long and ca 0.5-0.8 mm wide, glandular-pilose and hirsute-hispid; calyx cupuliform, lobed to about or to slightly below the middle, 5-6 mm long, sparsely glandular-pilose and hirsute-hispid, the lobes deltoid, acute; petals cuneate-obovate, shortly unguiculate, rounded at the apex, 10-15 mm long, yellow; staminal tube about ½ as long as the corolla, antheriferous throughout; style longer than the staminal tube, the stigmas capitellate and fimbrillate. *Mericarps* triquetrous-obovoid, obtuse and muticous or sometimes short-mucronulate at the apex, 3-4 mm long, cartilagi-

nous, foveolate-rugose, very minutely tuberculate; seeds trigonous-reniform, ca 2.5 mm long, minutely puberulus.

West Indies and Mexico to Argentina; moist thickets, brushy slopes and roadsides.

BOCAS DEL TORO: Changuinola Valley, Spur 12, *Dunlap 424* (F). CANAL ZONE: nr Gatun, *Standley 27331* (US); Barro Colorado Island, *Shattuck 731* (F, MO), *Wetmore & Abbe 150* (F); Obispo *Standley 31796* (US); Gamboa, *Standley 28315* (US); around Culebra, alt 50-150 m, *Pittier 2140* (US); Río Paraíso, above East Paraíso, *Standley 29863* (US); Río Pedro Miguel, nr East Paraíso, *Standley 29977* (US); nr Miraflores Locks, *J. M. & M. T. Greenman 5178* (MO); COCLÉ: El Valle de Antón, alt 600 m, *Allen 2253* (MO, US), 4221 (MO). DARIEN: along the Sambú River, above tide limit, *Pittier 5535* (US). PANAMA: between Capira and Potrero, alt 80-130 m, *Dodge & Hunter 8646* (F, MO, US); Agricultural Experiment Station at Matías Hernández, *Pittier 6879* (US); between Matías Hernández and Juan Díaz, *Standley 32049* (US); Taboga Island, *Miller 1961* (MO, US).

7. PAVONIA SIDIFOLIA H. B. K., Nov. Gen. Sp. Pl. **5:** 283. 1822.

Asterochlaena sidifolia (H. B. K.) Hassler, Repert. Sp. Nov. **8:** 114. 1910.

Suffrutex or shrub up to 1.2 m high, the stem glandular-pilose and stellate-puberulus to stellate-velutinous. *Leaves* rather long-petiolate, the petiole terete, up to 4 cm long, glandular-pilose and stellate-puberulus to stellate-velutinous, the stipules subulate-filiform; blade ovate, cordate at the base, acute to acuminate at the apex, crenate-serrate at the margin, up to 8 cm long and 5 cm wide, discolorous, green above and whitish beneath, 7- to 9-palminerved, stellate-puberulus and sometimes also glandular-pilose on the upper surface, stellate-tomentellous or stellate-velutinous and with the venation prominent on the lower surface. *Flowers* solitary in the upper leaf axils, long-pedicellate, the pedicel slender, articulated below the apex, up to 7 cm long, stellate-puberulus to stellate-tomentellous and with some long, simple hairs above the articulation, sometimes also glandular-pilose; epicalyx of 6-9 bractlets, these distinct, narrowly ovate, short-unguiculate, long-acuminate at the apex, 10-20 mm long and 2.5-5 mm wide, stellate-tomentellous and with some long, simple hairs along the margin; calyx cupuliform, lobed to about the middle, 5-10 mm long, stellate-tomentellous, the lobes deltoid, acute; petals cuneate-obovate, short-unguiculate, rounded at the apex, 18-25 mm long, yellow, reddish at the base; staminal tube short, about $\frac{1}{3}$ as long as the corolla, dentate, antheriferous throughout; style slightly longer than the staminal tube, the stigmas capitate and fimbrillate. *Mericarps* triquetrous-obovoid, gibbously obtuse and muticous at the apex, convex and longitudinally carinate dorsally, 3-4 mm long, coriaceous, inconspicuously rugose-reticulate, sparsely and very minutely tuberculate-papillate; seeds trigonous-reniform, ca 2.5-3 mm long, glabrous.

Panama, Venezuela to Peru.

LOS SANTOS: Monagre Beach, in field at edge of beach, *Dwyer 4154* (MO).

This is the first collection of *P. sidifolia* in Panama, as well as in North America; it can be referred to the subsp. *diuretica* (St.-Hil.) Gürke in Mart., Fl. Bras. **12**(3): 509. 1892 (*P. diuretica* St.-Hil., Pl. Us. Bras. *pl.* 53. 1827).

8. PAVONIA SPICATA Cav., Mon. Cl. Diss. Dec. 136, *t. 46(1)*. 1787.—Fig. 6 (C).

Malache scabra Vogel in Trew, Pl. Select. 50, *t. 90*. 1772.
Althaea racemosa Sw., Nov. Gen. Sp. Pl. Prodr. 102. 1788.
Pavonia racemosa (Sw.) Sw., Fl. Ind. Occ. 1215. 1800.
P. scabra (Vogel) Ciferri, Atti Ist. Bot. Univ. Pavia, ser. 6, **8:** 321. 1936, nomen illegitimum, non *P. scabra* Presl (Rel. Haenk. **2:** 129. 1835).

Shrub or infrequently small tree up to 5 m high, the stem sparingly branched, minutely stellate-puberulus to glabrescent. *Leaves* long-petiolate, the petiole terete, 3-8 cm long, minutely stellate-puberulus, the stipules linear-ovate; blade ovate to broadly ovate, cordate at the base, generally long-acuminate at the apex, entire or sinuate and often sparingly denticulate at the margin, 8-14 cm long and 5-9 cm wide, 5(-7)-palminerved, scabridulous and sparsely stellate-puberulus to glabrescent on both sides, the venation slightly prominent beneath. *Flowers* in elongate, lax, terminal racemes, sometimes somewhat crowded and subcorymbose at the apex, the pedicel slender, short to elongate and up to 5 cm long, stellate-puberulus to stellate-tomentellous; epicalyx of 6-10 bractlets, these distinct or nearly so, narrowly ovate, acute, shorter than to equalling the calyx, infrequently slightly longer than the calyx, 7-14 mm long and 2-3 mm wide, sparsely stellate-puberulus; calyx cupuliform, lobed to about the middle, 10-13 mm long, sparsely stellate-puberulus, the lobes broadly ovate to rotund, apiculate or short-acuminate; petals cuneate-obovate, rounded to truncate at the apex, 15-22 mm long, cream-colored or greenish-yellow; staminal tube nearly as long as the corolla, lobulate, sparsely papillate, antheriferous on the upper ⅓, the filaments up to 4 mm long, the upper filaments exceeding slightly the corolla; style slightly longer than the staminal tube, the stigmas capitate. *Mericarps* triquetrous-obovoid, with 3 broad, apical crests, one at each corner, dorsally convex and prominently rugose-reticulate, 8-11 mm long, coriaceous, glabrous; seeds trigonous-reniform, 4.5-5 mm long, glabrous.

Southern Florida, West Indies and Central America to northern South America; usually littoral, growing in association with mangroves.

BOCAS DEL TORO: Tidal flat nr Garey Creek, SE of Almirante across bay, *McDaniel 5159* (MO); Isla Colón, *von Wedel 41* (MO); Water Valley, *von Wedel 738* (MO); Old Bank Island, *von Wedel 1997* (MO, US); Fish Creek Hills, *von Wedel 2417* (MO, US); vic of Chiriquí Lagoon, *von Wedel 2915* (MO, US); s. loc., *von Wedel 503* (MO). CANAL ZONE: vic of Fort Sherman, *Standley 31179* (US). COLÓN: along the Río Culebra, above Santa Isabel, nr sea level, *Pittier 4168* (US).

9. PAVONIA RHIZOPHORAE Killip, Leafl. West. Bot. **7:** 118. 1954.—Fig. 6 (D).

Shrub 0.5-1.8 m tall (sometimes arborescent?), the stem unbranched or branched above, stellate-puberulus, soon glabrescent. *Leaves* rather long-petiolate, the petiole terete, 1-7 cm long, stellate-puberulus, the stipules narrowly oblong-ovate and acute; blade narrowly ovate or narrowly oblong-ovate, rounded to subcordate at the base, acute to long-acuminate at the apex, sparingly denticulate to dentate at the margin, 5.5-15 cm long and 1.5-5.5 cm wide, 3- to 5-palminerved, sparsely and minutely stellate-puberulus on both sides, the venation reticulate, prominulous above and prominent beneath. *Flowers* in elongate, terminal racemes, rather long-pedicellate (at least the lower flowers), the pedicel stout, up to 2 cm

long, stellate-tomentellous to stellate-puberulus; epicalyx of 5-8 bractlets, these nearly distinct, narrowly oblong-ovate, acute to acuminate, 7-10 mm long and 1.5-3 mm wide, stellate-puberulus; calyx campanulate, lobed to about the middle, 10-15 mm long, stellate-puberulus, the lobes deltoid-ovate, acute; petals narrowly obovate-spatulate, rounded-truncate at the apex, 20-28 mm long, yellow or greenish-white; staminal tube nearly equalling the corolla, 5-lobulate at the apex, papillate, antheriferous on the upper ⅓, the filaments 4-6 mm long; style slightly longer than the staminal tube, the stigmas discoid. *Mericarps* triquetrous-subobovoid with a single, stout, triangular, apical cusp ca 3 mm long, sometimes also with 2 prominulous apical and distal crests, strongly longitudinally carinate, the keel extending to the base of the cusp, and rather obscurely rugulose-reticulate dorsally, the body up to 9 mm long, coriaceous, glabrous; seeds reniform, ca 5 mm long, very minutely papillate.

Panama (southern Darien) and Colombia (Dept El Valle and Choco).

DARIEN: Puerto St. Dorotea, on bank of creek nr ocean, *Dwyer 2286* (MO).

Originally described from Colombia, this is the first collection of *P. rhizophorae* in Panama as well as in North America. Like the closely related *P. spicata* this species is littoral and grows in association with mangroves.

10. PAVONIA FRUTICOSA (Mill.) Fawcett & Rendle, Fl. Jamaica **5:** 130. 1926.—Fig. 6 (E).

Sida fruticosa Mill., Gard. Dict. ed. 8. 1768.
Urena typhalaea L., Mant. Pl. 258. 1771.
Pavonia typhalaea (L.) Cav., Mon. Cl. Diss. Dec. 134. 1787, 350, *t. 197*. 1788.

Herb or shrub up to 2 m high, the stem simple or few-branched, stellate-puberulus. *Leaves* with the petiole 0.5-5 cm long, minutely stellate-puberulus, the stipules subulate-ovate, acuminate; blade narrowly elliptic to elliptic, or narrowly obovate to obovate, cuneate to rounded (exceptionally subcordate) at the base, more or less acuminate at the apex, coarsely crenate-dentate or crenate-serrate at the margin, up to 20 cm long and 10 cm wide, 1- to 3-nerved at the base, sparsely and minutely stellate-puberulus on both sides, the venation slightly prominent beneath. *Flowers* mostly in small, dense, corymbiform or subcapitate inflorescences at the apex of the stem or branchlets, the bracts ovate-lanceolate, acuminate; pedicel ca 5 mm long; epicalyx of 5-6 bractlets, these united for less than ¼ of their length, narrowly ovate, acuminate, 5.5-11 mm long and 1.5-3 mm wide, sparsely and minutely stellate-puberulus; calyx tubular, lobed to about the middle, 4-7 mm long, stellate-puberulus, the lobes ovate-triangular, acute, ciliolate at the margin; petals narrowly obovate-cuneate, asymmetrical, rounded at the apex, 10-13 mm long and ca 4 mm wide, white (exceptionally pink?); staminal tube ca 6-8 mm long, 5-lobulate at the apex, antheriferous near the apex, the filaments few and ca 1 mm long; style slightly longer than the staminal tube, the stigmas capitellate and minutely fimbrillate. *Mericarps* triquetrous, 5-7 mm long and ca 2.7 mm wide, rigid-chartaceous, the back convex, nearly smooth, glabrous and with 3 inconspicuous, longitudinal ribs, 1 central and 2 marginal, the apex rounded and with

3 proximate, retrorsely hispidulous awns, the central up to 7.5 mm long, the lateral shorter; seeds trigonous, up to 5 mm long, glabrous.

West Indies and Panama to Peru, Brazil and Paraguay; in moist soil, at edges of forests and in wooded swamps.

CANAL ZONE: between Chagres Batteries and Fort San Lorenzo, Fort Sherman Military Reservation, *Maxon & Valentine 7027* (US); vic of Fort Sherman, *Standley 31042* (US); nr Gatun, *Goldman 1873* (US); Las Cascadas Plantation, nr Summit, *Standley 29593* (US); Chiva-Chiva trail 2 mi above Red Tank, *Maxon & Harvey 6587* (US). CHIRIQUÍ: 6 mi N of Concepción, *Ebinger 758* (MO). DARIEN: S of El Real, *Duke 5049* (MO); ca 10 mi S of El Real on Río Pirre, path from Pucro to Río Pucro, *Duke 5367* (MO); Paya to Pucro, *Stern et al. 237* (MO); vic of Caná, alt 1750 ft, *Stern et al. 469* (MO, US); s. loc., *Sexton 112A* (MO), *112B* (MO). PANAMA: Juan Díaz, *Standley 30463* (US); nr the big swamp E of the Río Tocumen, *Standley 26629* (US); along road between Panama and Chepo, *Dodge et al. 16668* (MO); ca 6 mi E of Chepo on Pan-Am. Highway, *Duke 4084* (MO); Río Tartaré, *Woodson & Schery 1014* (MO). SAN BLAS: Perme, *Cooper III 262* (F, US); Isla de Aligandi, *Dwyer 6843* (MO). PROVINCE UNKNOWN: *Hayes 101* (MO).

11. Pavonia spinifex (L.) Cav., Mon. Cl. Diss. Dec. 133, *t.45(2)*. 1787.

Hibiscus spinifex L., Syst. Nat. ed. 10, 1149. 1759.

Shrub, small or large and straggling, the stem up to 5 m high but usually much shorter, sparsely to rather copiously stellate-puberulus. *Leaves* with the petiole 0.5-6 cm long, more or less densely stellate-puberulus, the stipules subulate-linear; blade ovate, oblong-ovate to narrowly oblong-ovate, rounded, truncate or more or less deeply cordate at the base, acute to more or less acuminate at the apex, irregularly and coarsely serrate-dentate or dentate-crenate at the margin, 4-12 cm long and 2-8 cm wide, 3- to 5-palminerved, scabridulous and stellate-puberulus on both sides, the venation slightly prominulous above and prominulous beneath. *Flowers* axillary, solitary or somewhat clustered on short branchlets, the pedicel short to elongate, up to 5 cm long, more or less densely stellate-puberulus; epicalyx of 5-8 bractlets, these nearly distinct, narrowly oblong-linear, somewhat constricted toward the base, acute at the apex, 9-12 mm long and 0.8-1.3(2.5) mm wide, stellate-puberulus and ciliate at the margin; calyx cupuliform at the base, lobed to below the middle, 9-13 mm long, stellate-puberulus, the lobes narrowly triangular-ovate, acute to acuminate, 6-9 mm long and 2.5-4 mm wide at the base, ciliate at the margin; petals obovate-cuneate, unguiculate, 2-4 cm long and 1.5-2.5 cm wide, yellow; staminal tube nearly equalling the corolla, lobulate-dentate, antheriferous on the upper ⅓, the filaments ca 2-2.5 mm long; style branches exceeding the staminal tube, the stigmas capitellate and fimbrillate. *Mericarps* broadly triquetrous-obovoid, 4-6 mm long, rigid-chartaceous, the back convex, prominently reticulate, setose at the apex and with 3 longitudinal ribs, 1 central and 2 marginal, each bearing a very stout, retrorsely setose awn up to 10 mm long, the central awn apical, the lateral markedly below the apex; seeds trigonous-reniform, 2.5-4 mm long, glabrous.

Southeastern United States, West Indies and Mexico to Brazil and Peru.

This species was reported by Hemsley (Biol. Centr.-Am. **1:** 117. 1879) and by Gürke (in Mart., Fl. Bras. **12**(3): 481. 1892, under subsp. *genuina* Gürke) to have been collected in Panama by Seemann and by Duchassaing, respectively.

Fig. 7. PAVONIA OXYPHYLLARIA J. D. Sm.: A, habit (× ⅔); B, flower (ca × 2); C, androecium and pistil (× 5⅓); D, fruit (× 2). After *Allen 2742.*

12. PAVONIA OXYPHYLLARIA J. D. Sm., Bot. Gaz. **23:** 237. 1897.—Fig. 7.

Pavonia costaricensis Hochr., Ann. Conserv. Jard. Bot. Genève **10:** 18. 1906.
Malache fulva Standley, Contr. U. S. Nat. Herb. **18:** 115. 1916.
Pavonia fulva (Standley) Standley, Field Mus. Nat. Hist., Bot. Ser. **4:** 231. 1929.

Herb or shrub up to 1 m high, the stem flexuous, whitish-stellate-puberulus and copiously hispid with up to 4 mm long, mostly simple, fulvous hairs. *Leaves* very short-petiolate, the petiole stout, up to 9 mm long, densely fulvous-hispid, the stipules subulate; blade generally slightly asymmetrical, narrowly elliptic or narrowly oblong-ovate, usually slightly oblique at the base, gradually long-acuminate at the apex, serrate at the margin, up to 17 cm long and 5.5 cm wide, chartaceous, 3(-4)-palminerved, abundantly hispid on both surfaces, the venation prominent beneath. *Flowers* solitary (or sometimes binate?) in the upper leaf axils, long-pedicellate, the pedicel slender, 2-8.5 cm long, whitish-stellate-puberulus and densely fulvous-hispid; epicalyx of 11-13 bractlets, these distinct, linear-subulate, 15-20 mm long, fulvous-hispid; calyx cupuliform, shortly and broadly dentate, 2.5-4 mm long, stellate-tomentellous and with a few, long setae near the apex; petals obovate-cuneate, 10-12 mm long, white; staminal tube ca 6 mm long, lobulate, antheriferous below the apex, the filaments very short; style branches exceeding the staminal tube, the stigmas capitate and minutely fimbrillate. *Mericarps* broadly triquetrous-obovoid, ca 6 mm long and 4-5 mm wide, rigid-chartaceous, the back convex, prominently reticulate, glabrous and with 3 longitudinal ribs, 1 central and 2 marginal, each bearing a long, retrorsely hispidulous awn, the awns apical or nearly so, not proximate, 9-12 mm long; seeds trigonous-reniform, ca 4-4.5 mm long, minutely puberulus.

Costa Rica, Panama, Colombia, Brazil and Peru.

BOCAS DEL TORO: vic of Chiriquí Lagoon, *von Wedel 1099* (MO). COCLÉ: La Mesa, *Allen 2742* (MO).

13. PAVONIA PENDULIFLORA (Standley) Standley, Field Mus. Nat. Hist., Bot. Ser. **4**: 231. 1929.—Fig. 6 (F).

Malache penduliflora Standley, Contr. U. S. Nat. Herb. **18**: 117. 1916.

Shrub 1-2.5 m high, the stem slender, branched, more or less densely puberulus with stiff, tawny, stellate hairs. *Leaves* short-petiolate, the petiole stout, up to 12 mm long, densely stellate-hirtellous, the stipules linear-subulate; blade asymmetrical, oblong-elliptic to elliptic, oblong-ovate or sometimes obovate, oblique at the base, gradually long-acuminate at the apex, serrulate to denticulate at the margin, up to 20 cm long and 7.5 cm wide, 3- to 4- to 5-palminerved, scabridulous or not, more or less densely stellate-hirtellous on both sides, the indumentum always denser on the lower surface, the venation prominulous beneath. *Flowers* axillary, solitary, pendulous (always?), long-pedicellate, the pedicel slender, generally slightly geniculate above the middle, 3-5 cm long, densely stellate-hirtellous, the fruiting pedicel up to 10 cm long; epicalyx of 8-10 bractlets, these nearly distinct, narrowly ovate, acute, 5.5-7 mm long and 0.8-1.5 mm wide, more or less densely stellate-hirtellous; calyx campanulate, lobed to about the middle, 6.5-8 mm long, more or less densely stellate-hirtellous, the lobes deltoid, acute, 3.5-4 mm long and 2-3.5 mm wide at the base; petals obovate-cuneate, asymmetrical, rounded-truncate to rounded-crenulate at the apex, 14-16 mm long and 9.5-11 mm wide, pink; staminal tube 5-dissected at the apex, 7.5-9 mm long, antheriferous on the upper ⅓, the filaments maximum 1 mm long; style branches exceeding the staminal tube,

the stigmas capitellate and minutely fimbrillate. *Mericarps* broadly triquetrous-obovoid, ca 8 mm long and 5.5 mm wide, rigid-chartaceous, the back convex, reticulate, glabrous and with 3 prominulous, longitudinal ribs, 1 central and 2 marginal, each bearing a stout, retrorsely hispidulous awn, the central awn apical and 7-8 mm long, the marginal markedly below the apex, shorter or not and 5.5-8 mm long; seeds trigonous-reniform, 6-7 mm long, glabrous.

Endemic to the Province of Chiriquí, where it grows in humid forest at high elevations up to 2000 m.

CHIRIQUÍ: vic of Casita Alta, Volcán de Chiriquí, alt ca 1500-2000 m, *Woodson et al. 983* (F, MO); around Los Signas Camp, southern slope of Cerro de la Horqueta, alt ca 1700 m, *Pittier 3188* (holotype US); Cerro Horqueta, alt 6500 ft, *Christine & W. von Hagen 2041* (NY); Bajo Chorro, alt 1900 m, *M. E. Davidson 54* (F, MO, US), *Woodson & Schery 662* (MO), *705* (MO); vic of Bajo Mona and Quebrada Chiquero, alt 1500 m, *Woodson & Schery 529* (MO, US); Palo Alto, just E of Boquete, alt 5000 ft, *Stern et al. 1033* (MO, US); slope of Sierra Boquete, alt 4500 ft, *Bro. Maurice 877* (MO, US); along the Río Ladrillo, above El Boquete, *Pittier 3287* (US).

14. PAVONIA LONGIPES Standley, Field. Mus. Nat. Hist., Bot. Ser. **18:** 672. 1937.

Herb or suffrutex up to 1 m high, the stem sparsely stellate-puberulus or long-hirsute with simple, fulvous hairs. *Leaves* with the petiole stout, 1-8 cm long, more or less densely appressed-stellate-puberulus or long-hirsute and with mostly simple hairs or with both indumenta intermixed, the stipules linear-subulate; blade narrowly elliptic, narrowly obovate or narrowly oblong-obovate, rounded to obtuse or narrowly cordate at the base, gradually long-acuminate or acute at the apex, serrulate to serrate at the margin, up to 24 cm long and 9 cm wide, 1- to 3(-5)-palminerved, with both surfaces sparsely appressed-stellate-puberulus or stellate-puberulus and long-hirsute, the simple hairs mostly along the veins, the venation prominent beneath. *Flowers* in dense, few-flowered fascicles, these axillary and solitary or disposed along well-developed flowering branches, usually long-pedunculate, the flowering branches and peduncles sparsely appressed-stellate-puberulus or sparsely to densely long-hirsute, the flowers subsessile or the pedicel up to 15 mm long, the bracts usually deeply 3-lobed; epicalyx 6-8.5 mm long, composed of 8-10 bractlets united at the base for ca ⅓-½ of their length, linear-lanceolate, acute, short- to long-hirsute, the hairs mostly simple; calyx campanulate, ca 3 mm long, membranous, glabrous except the pilosulose margin of the lobes, these deltoid to broadly deltoid, acute to more or less obtuse, ca 1-1.3 mm long and 1.2-2.5 mm wide at the base, the sinuses acute to rounded; petals obovate-cuneate, ca 7 mm long, purple (cf. Standley, loc. cit.) or white; staminal tube slightly shorter than the corolla, 5-lobulate at the apex, antheriferous below the apex, the filaments few and up to 1 mm long; style branches exceeding the staminal tube, the stigmas capitellate and minutely fimbrillate. *Mericarps* narrowly triquetrous, 6-8 mm long and 2-2.3 mm wide, rigid-chartaceous, the back slightly rugose-reticulate, glabrous or minutely papillate near the apex and with 3 slightly raised longitudinal ribs, 1 central and 2 marginal, each bearing a retrorsely hispidulous awn, the awns apical, not proximate, the central 4-5 mm long, the marginal 3-4 mm long; seeds narrowly ovate, ca 5 mm long, glabrous.

Costa Rica and Panama.

This species is represented in Panama by two varieties, which can be distinguished as follows:

a. Stem, leaves, peduncles and pedicels appressed-stellate-puberulus; leaf blades rounded to obtuse at the base; epicalyx short-hirsute; calyx lobes broadly deltoid, more or less obtuse, the sinuses rounded .... var. LONGIPES

aa. Stem, leaves, peduncles and pedicels long-hirsute with mostly simple, fulvous hairs intermixed or not with shorter, stellate hairs; leaf blades narrowly cordate at the base; epicalyx long-hirsute; calyx lobes deltoid, acute, the sinuses acute .... var. HIRSUTA

14a. PAVONIA LONGIPES var. LONGIPES.

BOCAS DEL TORO: vic of Chiriquí Lagoon, Darkland, *von Wedel 2617* (MO); Changuinola Valley, *Dunlap 408* (type, F, US).

14b. PAVONIA LONGIPES var. **HIRSUTA** A. Robyns, var. nov.

A var. *longipede* cauli, foliis, pedunculis pedicellisque longe hirsutis pilisque plerumque simplicibus fulvis et interdum pilis brevioribus et stellatis intermixis, foliorum lamina basi anguste cordata, involucro longe hirsuto calycisque lobis deltoideis acutis et cum sinibus acutis sat recedit.

DARIEN: S of El Real, *Duke 5849* (MO); vic of Pinogana, alt ca 20 m, *Allen 931* (MO); nr the mouth of Río Yape, alt ca 20 m, *Allen 362* (holotype MO, isotype F); bank above Río Paca, *Stern et al. 587A* (MO).

15. PAVONIA ROSEA Schlecht., Linnaea **11:** 355. 1837.

Herb, suffrutex or shrub up to 1.5 m high, the stem simple or rather freely branched, covered with short stellate-hairs or rather hirsute with simple and stellate hairs especially when young. *Leaves* with the pedicel 0.5-6 cm long, stellate-puberulus or hirsute, the stipules linear-subulate; blade polymorphic, obovate to narrowly obovate or elliptic to oblong-elliptic, cuneate, obtuse or slightly cordate to narrowly subcordate at the base, acute or short- to long-acuminate at the apex, coarsely to rather finely serrate or dentate at the margin, up to 17 cm long and 8 cm wide, 3(-5)-palminerved, rough or not, stellate-puberulus or hirsute with simple and stellate hairs on both sides, the indumentum denser beneath, the venation prominent on the lower surface. *Flowers* in few-flowered corymbiform or loosely capituliform inflorescences, the peduncles terminal or axillary, generally elongate and up to 15 cm long, stellate-puberulus or hirsute, rarely flowers axillary and solitary, the pedicel up to 15 mm long, stellate-puberulus or hirsute, the bracts entire or 3-lobed almost to the base, linear-lanceolate; epicalyx of 7-11 bractlets, these united at the base for maximum ¼ of their length, adnate to the base of the calyx, linear-lanceolate, acute, 5.5-11 mm long and 0.5-1.5 mm wide, stellate-puberulus and/or hirsute with simple and/or stellate hairs; calyx campanulate, lobed to about the middle or the lobes shorter, 3-5 mm long, stellate-puberulus and generally with few, hirsute hairs along the margin, the lobes deltoid, acute; petals obovate-cuneate to oblong-obovate, asymmetrical, rounded to somewhat undulate at the apex, 8-13 mm long and 3-6 mm wide, rose or white; staminal tube slightly

to much shorter than the corolla, 5-7 mm long, 5-lobulate at the apex, antheriferous below the apex, the filaments few, ca 0.7-0.8 mm long; style branches exceeding slightly the staminal tube, the stigmas capitate and densely fimbrillate. *Mericarps* triquetrous-obovoid, 5-7 mm long and ca 2.5-3.5 mm wide, rigid-chartaceous, the back convex, smooth to lightly reticulate, glabrous or sparsely and minutely papillate near the apex and with 3 prominulous ribs, 1 central and 2 marginal, each bearing a retrorsely hispidulous awn, the central awn apical and 3.5-6 mm long, the marginal below the apex and 2.5-5 mm long; seeds trigonous, 4-5 mm long, glabrous.

The species is represented in Panama by two varieties, distinguished as follows:

a. Indumentum of mostly short, stellate hairs; petals white or pink; at low altitudes .... var. ROSEA

aa. Indumentum of rather long, hirsute hairs, these simple or stellate; petals pale to deep pink; at high altitudes, between 1200-1900 m .... var. MAXONII

15. PAVONIA ROSEA var. ROSEA.—Fig. 6 (G).

West Indies and Mexico to Colombia and Brazil; moist woods and llanos, often growing as a weed, at low altitudes.

BOCAS DEL TORO: Isla Colón, SW of Bocas at Macaw Hills, alt 0-120 m, *von Wedel 540* (MO); Old Bank Island, vic of Chiriquí Lagoon, *von Wedel 2003* (MO, US); Water Valley *von Wedel 856* (MO); in Laguna de Chiriquí and its neighborhood, *Hart 135* (US); Changuinola Valley, *Dunlap 239* (US), *Dwyer 2107* (MO), *Stork 281* (US); s. loc., *Carleton 270* (US), *von Wedel 149* (MO). CANAL ZONE: Barro Colorado Island, *Ebinger 551* (MO), *McDaniel 5004* (MO), *Standley 40852* (US), *Sr. Mary Victoria 7* (MO), *Woodson & Schery 985* (MO); Río Paraíso, above East Paraíso, *Standley 29862* (US); Balboa, *Standley 26054* (US). COCLÉ: Penonomé, *Dwyer 1099* (MO), *1998* (MO). DARIEN: Caná and vic, *R. S. Williams 830* (US). PANAMA: vic of Arenoso, lower Río Trinidad, alt 26-50 m, *Seibert 633* (MO); Río Pita, 1-3 mi above confluence with Río Maestra, *Duke 4772* (MO).

15b. PAVONIA ROSEA var. **MAXONII** (Standley) A. Robyns, stat. nov.

Malache maxonii Standley, Contr. U. S. Nat. Herb. **18**: 116. 1916.
Pavonia maxonii (Standley) Standley, Field Mus. Nat. Hist., Bot. Ser. **4**: 231. 1929.

Costa Rica and Panama. Restricted to the Province of Chiriquí in Panama and growing at high elevations between 1200-1900 m.

CHIRIQUÍ: Chiriquí Viejo Valley, *G. White 91* (F, MO); Valley of the upper Río Chiriquí Viejo, vic of Monte Lirio, alt 1300-1900 m, *Seibert 318* (MO); Llanos on slopes of Volcán de Chiriquí Viejo and along Río Chiriquí Viejo, alt 1200 m, *Allen 979* (MO, US); vic of Callejón Seco, Volcán de Chiriquí, alt 1700 m, *Woodson & Schery 482* (MO, US); Bajo Mono, elev 4500 ft, *M. E. Davidson 503* (F, MO, US); forest along the Río Ladrillo and vic, above El Boquete, alt 1200-1300 m, *Maxon 5394* (holotype US), *Pittier 3287 pro parte* (US).

10. MALVA L.

MALVA L., Sp. Pl. 687. 1753, Gen. Pl. ed.5, 308. 1754.

Herbs, sometimes more or less suffruticose, annual or perennial, the stems erect to decumbent or prostrate, glabrous or the indumentum of simple or stellate hairs. *Leaves* usually long-petiolate, the stipules caducous, the blades commonly more or

less circular-cordate in outline, crenate to serrate or shallowly to deeply palmatilobed or palmatidivided. *Flowers* axillary, solitary or in more or less dense glomerules; epicalyx of 3 distinct bractlets; calyx cupuliform, 5-lobed, persistent or accrescent; petals 5, obcordate-cuneate, connate at the base and adnate to the base of the staminal tube, the claws glabrous or ciliate; staminal tube divided at the apex into numerous filaments, the anthers reniform; ovary of more or less 10 free, 1-ovulate carpels, the ovules ascending; style branches isomerous with the carpels, linear, introrsely stigmatose. *Fruits* discoid, separating into many indehiscent mericarps, these verticillate around a central axis, reniform, muticous; seeds glabrous; embryo curved, the albumen scant.

An Old World genus of which several species have become naturalized as weeds in North and South America. A few species with relatively large and showy flowers are cultivated as ornamentals. Only one species is reported from Panama.

1. Malva neglecta Wallroth, Syll. Pl. Nov. (Ratisb.) **1:** 140. 1824.—Fig. 8.

Malva rotundifolia Auct. non L.

Herb, the stem commonly procumbent or trailing, usually branched, up to 2 m long, appressed-stellate-pubescent. *Leaves* with a slender petiole up to 20 cm long, rather sparsely stellate-pubescent, the stipules ovate, acute or acuminate, 4-7 mm long; blade circular or circular-reniform, deeply cordate, very shallowly several-lobed, ca 1-6 cm long and broad, the margins crenate-denticulate, 5- to 7-palminerved, strigose on both sides with simple or stellate hairs, densely so when young, the venation prominulous beneath. *Flowers* solitary or in loose, few-flowered clusters, the pedicel slender, 2-4 cm long, stellate-puberulus to stellate-tomentellous; epicalyx bractlets linear-ovate, acute, ca 4 mm long and 0.8 mm wide, stellate-puberulus and ciliolate along the margin; calyx ca 5-6 mm long, densely stellate-puberulus, lobed to or little beyond the middle, the lobes deltoid and acuminate, somewhat accrescent and enclosing the schizocarp; petals ca 12 mm long, the claws barbate, white and usually lavender toward the apex; androecium ca 6-7 mm long, the staminal tube sparsely and minutely stellate-puberulus; styles ca 8-9 mm long. *Fruit* ca 5-6 mm in diam, the mericarps 12-15, smooth, very minutely puberulus.

A weed of roadsides and waste ground, of almost world-wide distribution.

CHIRIQUÍ: Cerro Punta, alt ca 6025 ft, *P. White 200* (F, MO). PANAMA: San José Island, *Johnston 1154* (GH).

11. MALVASTRUM A. Gray

Malvastrum A. Gray, Mem. Am. Acad. Arts Sci., ser. 2, **4:** 21. 1849, nom. gen. conserv.

Malveopsis Presl, Bot. Bemerk. 18. 1844.

Herbs or shrubs, the stems erect, the indumentum of simple or stellate or malpighiaceous hairs. *Leaves* petiolate, the blade serrate to deeply lobed or parted. *Flowers* axillary, solitary or glomerate, or in terminal, few- to many-flowered in-

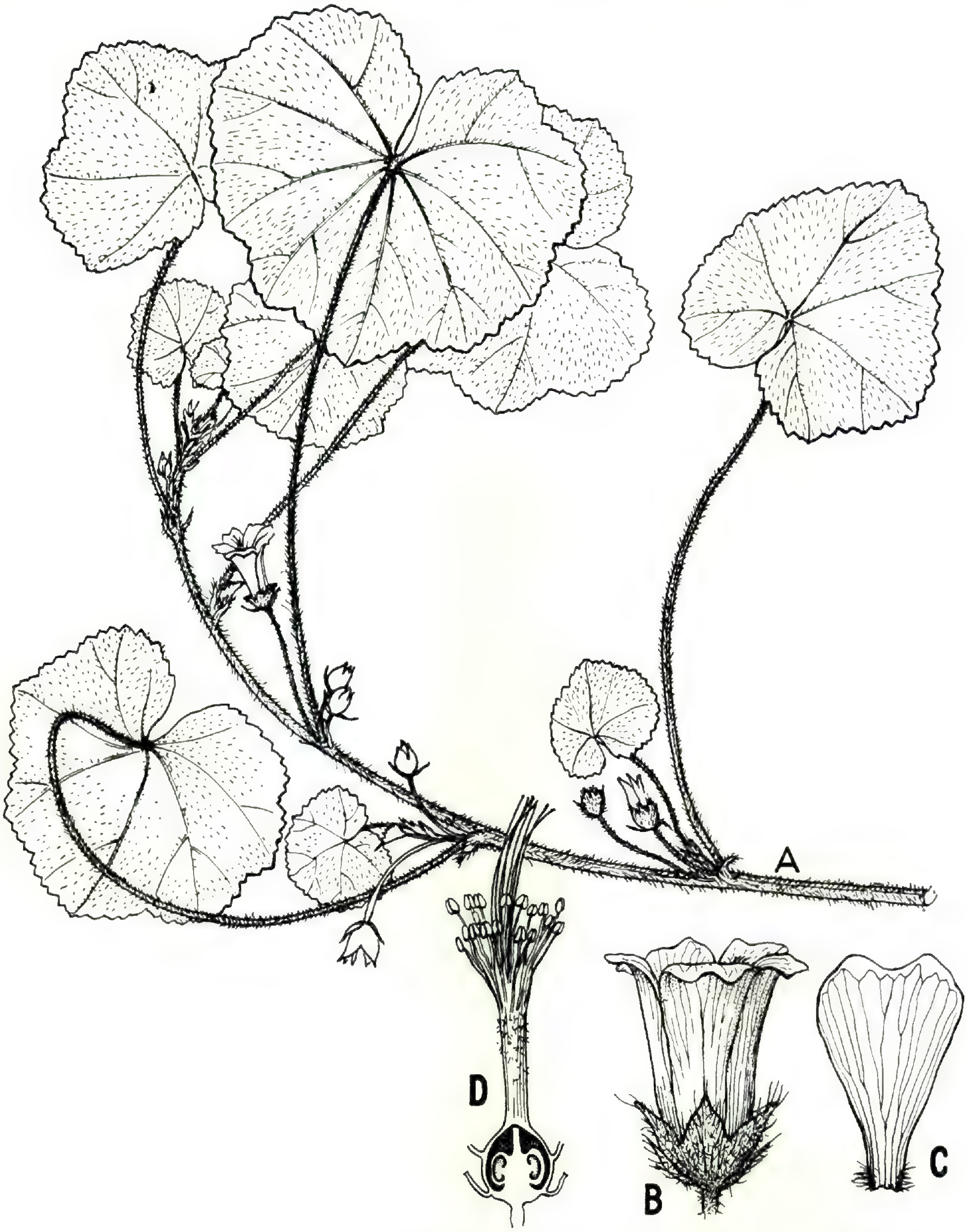

Fig. 8. MALVA NEGLECTA Wallroth: A, habit (ca × ⅔); B, flower (× 2⅔); C, petal (× 2⅔); D, androecium and pistil (ovary in longitudinal section) (× 5⅓). After *P. White 200.*

florescences, the individual flowers short-pedicellate to sessile; epicalyx of 3 distinct, narrow, persistent bractlets; calyx 5-lobed, accrescent and foliaceous in fruit; petals 5, obovate-cuneate, more or less asymmetrically emarginate at the apex, connate at the base and adnate to the base of the staminal tube, yellow; staminal tube divided at the apex into few to numerous filaments, the anthers reniform; ovary of

many, free, 1-ovulate carpels, the ovules erect or ascending; style branches isomerous with the carpels, filiform, the stigmas capitellate. *Fruits* discoid, composed of 1 whorl of mericarps, these hippocrepiform, incurved-rostrate to muticous, sometimes with 1 apical and 2 dorsal awns, nearly indehiscent; seeds glabrous; endosperm scanty; cotyledons plicate.

A genus of about 12 species of tropical and subtropical America, two of which are now widely distributed in both hemispheres and are the only species in Panama.

This genus is here treated from the point of view that *M. coromandelianum* (L.) Garcke (*M. carpinifolium* A. Gray) is the type species (cf. Kearney, Leafl. West. Bot. **5:** 23-24. 1947 & **7:** 238-241. 1955, & Am. Midl. Nat. **46:** 119-121. 1951).

a. Indumentum strigose, the hairs simple and 4-rayed, the rays approximate in pairs (malpighiaceous); flowers axillary, solitary or in glomerules; mericarps provided at the apex with an erect awn and with 2 short, dorsal awns near the middle .... 1. M. COROMANDELIANUM
aa. Indumentum stellate-tomentellous to stellate-puberulus; flowers in dense, terminal spikes; mericarps incurved-rostrate at the apex, unarmed .... 2. M. AMERICANUM

1. MALVASTRUM COROMANDELIANUM (L.) Garcke, Bonplandia **5:** 295. 1857.

Malva coromandeliana L., Sp. Pl. 687. 1783.
M. tricuspidata R. Brown in W. Aiton, Hort. Kew. ed. 2, **4:** 210. 1812.
Malvastrum carpinifolium A. Gray, Mem. Am. Acad. Arts Sci., ser. 2, **4:** 22. 1849.
M. tricuspidatum (R. Brown) A. Gray, Pl. Wright. Tex.-Neo-Mex. in Smiths. Contr. Knowl. **3**(5): 16. 1852.

Suffrutex or shrub up to 1.5 m high, covered with simple and 4-rayed, strigose hairs, the rays approximate in pairs. *Leaves* with the petiole slender, up to 2.5 cm long, strigose, the stipules lanceolate, acuminate, 5-10 mm long; blade oblong-lanceolate to rounded-ovate, broadly cuneate to sometimes truncate at the base, acute or obtuse at the apex, coarsely serrate, at the margin, 3-8 cm long, the nervation prominent beneath, strigose on both sides, the indumentum however denser on the lower surface. *Flowers* axillary, solitary or in glomerules, the individual flowers sessile or shortly pedicellate, the pedicel up to 5 mm long; epicalyx bractlets linear-subulate, acute, 3-6 mm long and 0.5-1 mm broad, hispid; calyx broadly campanulate, 5-costate, lobed to or slightly below the middle, 5-7 mm long, strigose, the lobes ovate, acuminate, ciliolate; petals 8-9 mm long and 4-6 mm broad, the claw barbate; androecium slightly shorter than the calyx, the staminal tube ca 3-3.5 mm long, glabrous; styles 5-6 mm long, connate in the lower part. *Mericarps* 10-12, dorsally sulcate, ca 2 mm long and 1-1.2 mm thick, the apex provided with an erect awn ca 1-1.5 mm long, with 2 short, dorsal awns ca 0.5 mm long near the middle, dorsally and in part laterally minutely stellate-puberulus and hispid toward the apex.

A widely distributed weed in tropical and subtropical regions of both hemispheres, but of American origin; moist thickets, brushy slopes and roadsides.

CANAL ZONE: vic of Ancon, *Piper 6015* (US). PANAMA: vic of Juan Franco Race Track, nr Panama, *Standley 27670* (US), *27691* (US); Agricultural Experiment Station at Matías Hernández, *Pittier 6712* (US); Taboga Island, *Standley 27837* (US). PROVINCE UNKNOWN: *Grisebach s.n.* (ded. 1857, MO 10125).

2. Malvastrum americanum (L.) Torrey, Bot. Bound. in Emory, Rep. U. S. & Mex. Bound. Surv. **2**(1): 38. 1859.—Fig. 9.

Malva americana L., Sp. Pl. 687. 1753.
M. spicata L., Syst. Nat. ed. 10, 1146. 1759.
Malvastrum spicatum (L.) A. Gray, Mem. Am. Acad. Arts Sci., ser. 2, **4**: 22. 1849.

Herb or suffrutex, perennial, the stem commonly branched above, up to 3 m high, stellate-tomentellous to stellate-puberulus. *Leaves* usually long-petiolate, the

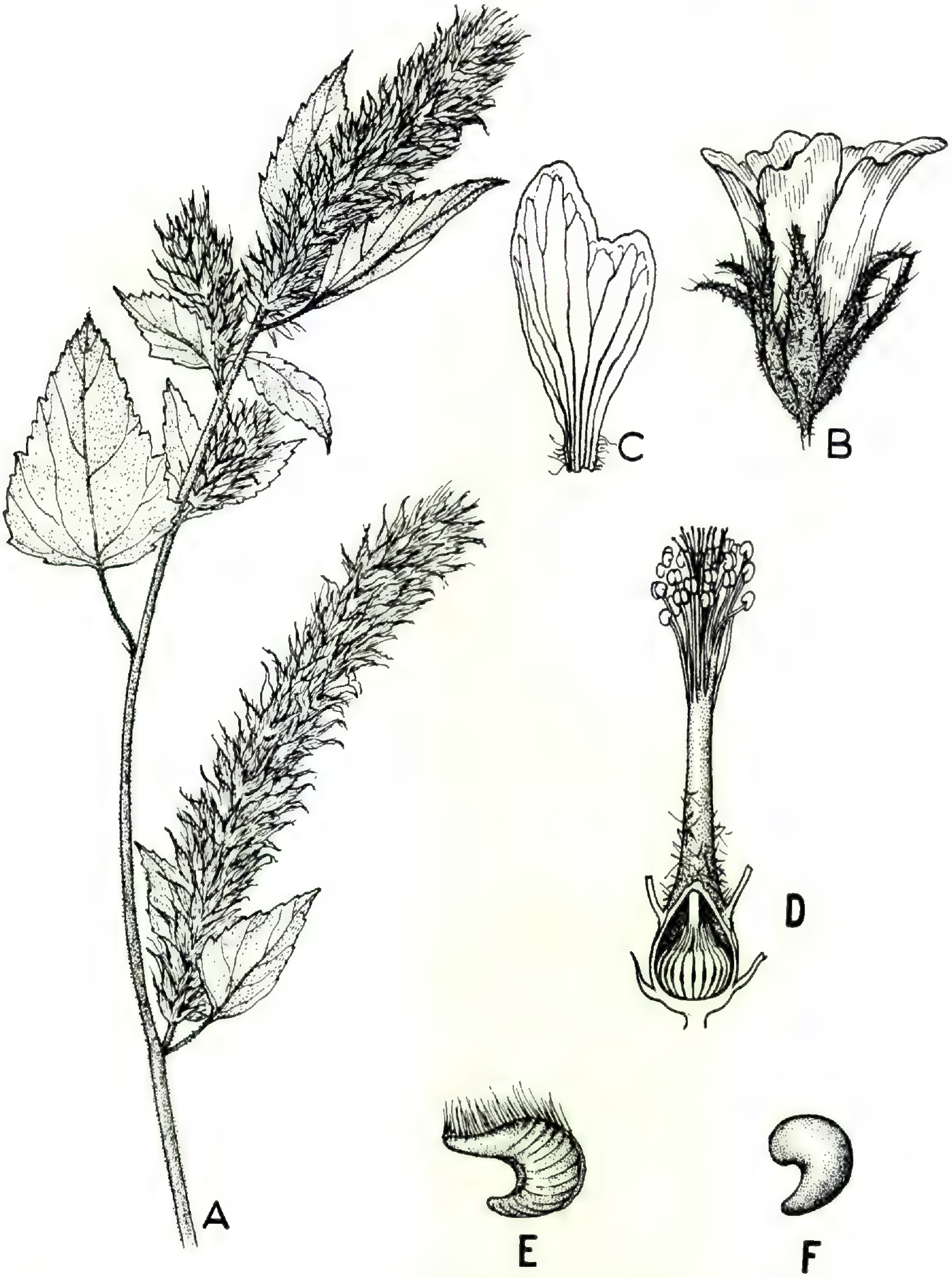

Fig. 9. Malvastrum americanum (L.) Torrey: A, habit (× ⅔); B, flower (× 5⅓); C, petal (× 5⅓); D, androecium and pistil (× 10⅔); E, mericarp (× 8); F, seed (× 8). After *Allen 4299*.

petiole up to 4 cm long, stellate-tomentellous to stellate-puberulus, the stipules subulate, 4-6 mm long; blade ovate, truncate, rounded or cuneate at the base, obtuse to acute at the apex, serrate at the margin, 2-7 cm long and 1.5-4.5 cm wide, stellate-puberulus on both sides, the indumentum however denser on the lower surface, the nervation prominent beneath. *Flowers* in dense, terminal spikes, these up to 14 cm long, the individual flowers sessile or nearly so; epicalyx bractlets narrowly ovate, acute or acuminate, 5-9 mm long and 1-1.3 mm broad, hispid; calyx campanulate, lobed to below the middle, 5-8 mm long, hispid, the lobes ovate, acuminate; petals 7-9 mm long and 3-4 mm wide, the claw barbate; androecium 3-5 mm long, the staminal tube stellate-pilose; styles 5-6 mm long, connate in the lower half. *Mericarps* 10-15, incurved-rostrate at the apex, 1.5-2 mm long and 0.8-1 mm thick, hispid toward the apex; seeds 1.2-1.5 mm long.

Probably of American origin but now distributed in tropical and subtropical regions of both hemispheres.

DARIEN: vic of Yape, Río Tuira, alt 25 m, *Allen 4299* (MO).

12. ANODA Cav.

Anoda Cav., Mon. Cl. Diss. Dec. 38. 1785.

Herbs or rarely suffrutices, glabrous or variously pubescent. *Leaves* petiolate, the stipules caducous, the blade often hastate or more or less palmatilobed. *Flowers* axillary and solitary or in terminal panicles or racemes, usually long-pedicellate; epicalyx wanting; calyx 5-merous, lobed, erect or spreading and greatly accrescent in fruit; petals 5, adnate to the base of the staminal tube, longer than the calyx, variously colored, often purple or blue; staminal tube dilated at the base, filamentiferous at the apex, the filaments numerous, the anthers reniform; ovary of 5-∞ carpels, each carpel 1-ovulate, the ovules pendulous or resupinate-horizontal; styles isomerous with the carpels, free at least in the upper part, the stigmas capitate or discoid. *Fruits* discoid or hemispherical, composed of a single whorl of mericarps, these rounded or umbonate to spurred dorsally, the lateral walls evanescent, the endocarp often detached from the pericarp and forming a partial or complete sac-like envelope around the seed or becoming fused with the outer seed coat; seeds glabrous or pubescent.

An exclusively American genus of about 13 species, monographed by Hochreutiner in 1916 (Ann. Conserv. Jard. Bot. Genève **20:** 29-68). Only one species is reported from Panama.

1. Anoda acerifolia DC., Prodr. **1** : 459. 1824.

Sida acerifolia Zuccagni in Roemer, Collectanea 148. 1809, nomen illegitimum, non (Cav.) Medic. (1787).
S. zuccagnii Spreng. in L., Syst. Veg. ed. 16, **3:** 121. 1826.
Anoda hastata Schlecht., Linnaea **11:** 214. 1837, non Cav. (1785).

Herb, annual, the stem erect or procumbent, up to 60 cm long, the younger parts sparsely hispid with long, simple, often reflexed hairs, and sometimes also sparsely and minutely stellate-puberulus. *Leaves* long-petiolate, the petiole 1.5-5

cm long, more or less densely hispid, the stipules subulate-filiform, 5-9 mm long; blade polymorphic, usually deltoid or angulate, hastately to more or less 5-palmatilobed, mostly truncate at the base, acute at the apex, coarsely few-serrate to entire at the margin, up to 7.5(-10) cm long and 6 cm broad, the upper leaves small, nearly concolorous, 5-palminerved, sparsely strigose and with simple hairs on both surfaces, the lower surface slightly paler and with the primary and secondary veins prominulous. *Flowers* axillary and solitary, long-pedicellate, the pedicel slender, 3-8 cm long, longer in fruit, sparsely hispid especially toward the apex, sometimes also with few minute stellate hairs; calyx broadly campanulate, lobed to slightly below the middle, ca 6-7 mm long, 10-nerved, sparsely strigose, much accrescent, up to 12-13 mm long and spreading in fruit, the lobes broadly triangular, acute, ca 3.5-4.5 mm long and 3 mm broad; petals oblong-obovate-cuneate, shallowly emarginate at the apex, 12-15 mm long and 7 mm wide, purple or bluish, ciliate at the base; androecium ca 5-6 mm long, the staminal tube ca 3-4 mm long, hispid; styles ca 5 mm long, connate halfway; ovary densely setose at the apex. *Fruit* discoid, ca 10-12 mm in diam, of 7-15 mericarps, these setose above, dorsally gibbous or beaked and with the beak up to 1 mm long, the pericarp bilamellar, the endocarp forming a white or yellowish fenestrate hood over the dorsum of the seed; seeds trigonous, ca 2.5 mm long, glabrous, dropping free at maturity.

Of infrequent occurrence throughout tropical and subtropical America, often of weedy habit; naturalized in the East Indies.

CANAL ZONE: around Frijoles, alt 10-30 m, waste places, *Pittier 2690* (US); Ancon, *J. M. & M. T. Greenman 5016* (MO).

13. SIDA L.

SIDA L., Sp. Pl. 683. 1753, Gen. Pl. ed. 5, 306. 1754.

Sidastrum Baker f., J. Bot. **30**: 137. 1892.

Herbs, shrubs or infrequently small trees, annual or perennial, glabrous or variously pubescent, the hairs mostly stellate. *Leaves* distichous or spiralled, subsessile to long-petiolate, the stipules persistent or caducous, the blade undivided to palmatilobed. *Flowers* axillary and solitary, or in paniculiform, racemiform, corymbiform or capitate inflorescences, subsessile to long-pedicellate, the pedicel sometimes adnate to the petiole of the subtending leaf or bract; epicalyx absent, the flowers in a few species subtended closely by stipule-like bracts (simulating an epicalyx); calyx 5-merous, terete or angulate, dentate or lobed, persistent to greatly accrescent; petals 5, often conspicuously oblique, adnate to the base of the staminal tube, usually yellow or orange; staminal tube dilated at the base, filamentiferous at the apex, the filaments few to numerous, the anthers reniform, usually everted; ovary of 5-∞ carpels, each carpel 1-ovulate, the ovules pendulous; styles isomerous with the carpels, free at least in the upper part, filiform, the stigmas capitellate or capitate. *Fruits* composed of a single whorl of mericarps usually separating freely from the axis and each other, the mericarps 3-gonous or 3-quetrous, apically muticous to 2-aristate, the dorsum smooth to rugose to muricate, the lateral walls

smooth or reticulate or rugose or clathrate, indehiscent or apically dehiscent, rarely dehiscent to the base dorsally or by breakdown of the lateral or basal walls; seeds glabrous or variously shortly pubescent; endosperm scanty or absent; embryo curved; cotyledons plicate or contortuplicate.

A genus of about 200 species of the warm-temperate and tropical regions, particularly well represented in the New World, with 16 species reported from Panama.

Useful references are:

Clement, I. D., Studies in *Sida* (*Malvaceae*). I. A review of the genus and monograph of the sections *Malacroideae, Physalodes, Pseudomalvastrum, Incanifolia, Oligandrae, Pseudonapaea, Hookeria* and *Steninda*. Contr. Gray Herb. Harvard Univ. **180:** 91 p. 1957.

Kearney, T. H., A tentative key to the North American species of *Sida* L. Leafl. West. Bot. **7:** 138-150. 1954.

———, A tentative key to the South American species of *Sida* L. Leafl. West. Bot. **8:** 249-270. 1958.

a. Pedicel adnate to the petiole of the subtending leaf or bract; mericarps 5-8 .... 1. S. CILIARIS

aa. Pedicel free.

b. Calyx greatly accrescent; stems prostrate, frequently rooting at the nodes; mericarps 5 .... 2. S. DECUMBENS

bb. Calyx persistent or moderately accrescent; stems usually erect (often decumbent in *S. jamaicensis*).

c. Leaf blades entire-margined; mericarps 7-9 .... 3. S. LINIFOLIA

cc. Leaf blades not entire-margined.

d. Mericarps more than 5[5-7(8) in *S. pyramidata* & (5)6-8 in *S. setifera*].

e. Flowers subtended by several subulate bracts longer than the calyx, the flowers thus appearing involucellate; mericarps 7-10, dehiscent to the base dorsally .... 4. S. QUINQUENERVIA

ee. Flowers not falsely involucellate; mericarps dehiscent at the apex.

f. Leaves distichous; stipules narrowly ovate to linear; mericarps 7-9(-12) .... 5. S. ACUTA

ff. Leaves spirally disposed; stipules linear-subulate or subulate.

g. Leaves long-petiolate, the blade ovate to broadly ovate; flowers glomerulate, short-pedicellate; calyx with the midribs and commissural ribs not thickened at the base.

h. Indumentum homotrichous, copiously puberulus with very minute, stellate hairs; calyx terete, 3.5-4 mm long; petals strongly oblique, 5-6(8) mm long; mericarps 5-7(8) .... 6. S. PYRAMIDATA

hh. Indumentum heterotrichous, finely stellate-tomentellous and generally with spreading hairs to 3 mm long; calyx 5-angulate, ca 7 mm long; mericarps (5)6-8 .... 7. S. SETIFERA

gg. Leaves short-petiolate, the blade often more or less rhombic, narrowly ovate, narrowly oblong-elliptic or narrowly oblong-obovate; flowers solitary, these toward the apex of the branches and branchlets often corymbose,

the pedicels usually elongate, filiform, up to 3.5 cm long; calyx with the midribs and commissural ribs markedly thickened at the base; mericarps (7)8-12(14) ..8. S. RHOMBIFOLIA

dd. Mericarps 5[5-7(8) in *S. pyramidata* & (5)6-8 in *S. setifera*].

i. Calyx terete, 2.7-4 mm long.

j. Flowers with capillaceous pedicels 1.5-4 cm long; calyx 2.7-3.5 mm long; petals crimson or purple, slightly oblique, 3.5-5 mm long; mericarps 5 ....9. S. PANICULATA

jj. Flowers short-pedicellate; calyx 3.5-4 mm long; petals yellow or orange, sometimes reddish at the claw, strongly oblique, 5-6(8) mm long; mericarps 5-7(8) ....6. S. PYRAMIDATA

ii. Calyx 5-angulate, 5-8 mm long.

k. Calyx with the midribs and commissural ribs not thickened at the base.

l. Leaves distichous.

m. Stipules narrowly ovate, attenuate-acuminate, 8-12 mm long and up to 4 mm wide, 3-5-several-nerved, persistent; mericarps glabrous; indumentum heterotrichous; stems usually erect ....10. S. GLOMERATA

mm. Stipules linear-subulate, ca 4-7 mm long, at length caducous; mericarps minutely stellate-tomentellous above; indumentum homotrichous; stems often decumbent ....11. S. JAMAICENSIS

ll. Leaves spirally disposed.

n. Leaf blades markedly cordate at the base; mericarps apically dehiscent.

o. Branchlets, petioles, pedicels and calyx shortly viscid-puberulus and sparsely hirsute with longer simple hairs ....12. S. GLUTINOSA

oo. Viscid indumentum wanting.

p. Flowers glomerate, subsessile or very short-pedicellate.

q. Indumentum finely stellate-tomentellous and generally also with long, yellowish hairs; calyx stellate-tomentellous and densely long-hirsute; staminal tube ca 4 mm long, the filaments numerous; mericarps 6-8, infrequently 5, minutely tomentellous toward the apex dorsally ....7. S. SETIFERA

qq. Indumentum rather sparsely hirsute with long, simple or few-armed, yellowish hairs, and often also with shorter stellate hairs; calyx hispid or subsetose on veins and along margins; staminal tube ca 2.5 mm long, the filaments relatively few; mericarps 5, glabrous or somewhat puberulus near the apex ....13. S. URENS

pp. Flowers solitary, the pedicels capillaceous, 1.5-2.5 cm long, up to 4.5 cm long in fruit ....14. S. GLABRA

nn. Leaf blades truncate or rounded at the base, infrequently shallowly subcordate; mericarps apically dehiscent but the seed escaping thru the disintegrated base ....15. S. SPINOSA

kk. Calyx with the midribs and commissural ribs markedly thickened at the base ....16. S. LINEARIFOLIA

1. SIDA CILIARIS L., Syst. Nat. ed 10, 1145. 1759.

Herb, perennial, or suffrutex, up to 45 cm high but usually shorter, the stem prostrate to ascending or erect, diffusely branched from the base, strigose-pubescent, often hirsute to tomentose toward the apex, the hairs mostly stellate or submalpighiaceous. *Leaves* with the pedicel geniculate at the apex, 3-9 mm long, hirsute and strigose-pubescent with stellate and submalpighiaceous hairs, the stipules linear to spatulate, acute to acuminate, 6-12 mm long, ciliate; blade small, very variable, mostly linear to narrowly oblong to oblong to ovate, sometimes subcircular, truncate to rounded or narrowly cordate at the base, acute to obtuse at the apex, to 2.5 cm long, the margins variably serrate above the base or only near and at the apex, sometimes merely 3-dentate apically, 3- to 5-palminerved, the upper surface glabrous or with few, appressed, simple or stellate hairs, the lower one more or less densely strigose-pubescent with stellate or submalpighiaceous hairs, and with the main veins prominulous. *Flowers* in terminal 2- to 8-flowered clusters, these subtended by the uppermost leaves and the hirsute-ciliate, stipule-like bracts, rarely axillary and solitary, the pedicel ca 1-2 mm long, adnate to the petiole of the subtending leaf or bract; calyx campanulate, terete, 5-7 mm long, villous with simple or stellate hairs or with both, persistent, the lobes triangular to narrowly ovate, acute, 2-4 mm long; petals obovate-spatulate to broadly rotund-triangular, more or less oblique, obtuse or retuse at the apex, 3-15 mm long and 2-10 mm wide, white, yellow, pink or purple, glabrous or sparsely puberulus at the base; staminal tube 3-5 mm high, glabrous or sparsely puberulus, the filaments 2-3 mm long; styles 4-8 mm long, connate below. *Mericarps* 5-8, trigonous, muticous to shortly 2-aristate apically, 2-3 mm high, chartaceous-coriaceous, the dorsum prominently muricate to rugose, glabrous to densely and minutely stellate-puberulus, the lateral walls rather coarsely reticulate; seeds trigonous-subrotund, ca 1.7 mm long, with scattered minute stellate hairs, these denser near the hilum.

A polymorphic species distributed from southern United States to Argentina and in the West Indies; savannas.

COCLÉ: Aguadulce, nr sea level, *Pittier 4843* (F, US); Natá, alt ca 50 m, *Allen 817* (F, MO, US); outside of Penonomé, *Ebinger 999* (MO). PANAMA: nr beach at Nueva Gorgona, *Duke 4488* (MO); Playa, nr Riomar, *Ebinger 493* (MO); nr Punta Paitilla, *Standley 26288* (US); Nuevo San Franscisco, *Standley 30786* (US); between Las Sabanas and Matías Hernández, *Standley 31863* (US).

Clement, in a recent paper (Contr. Gray Herb. Harvard Univ. **180:** 22-30. 1957), divides the species into five varieties which are, according to him (p.26), "only tendencies" in the species. In Panama, he recognizes two varieties: *S. ciliaris* var. *ciliaris* and var. *mexicana* (Moric.) Shinners, Field and Lab. **21:** 94. 1953 (*S. anomala* St.-Hil. var. *mexicana* Moric., Pl. Nouv. Am. 36, *t. 24.* 1837), the last variety being characterized by the narrow leaves and large flowers (cf. *Allen 817*). As, however, complete intergradation occurs between these two varieties, I think it is not necessary to maintain the infraspecific taxa.

2. SIDA DECUMBENS St.-Hil. & Naud., Ann. Sci. Nat., Bot., sér. 2, **18:** 51. 1842.

Anoda decumbens (St.-Hil. & Naud.) Hochr., Ann. Conserv. Jard. Bot. Genève **20:** 56. 1916.

Herb, the stem prostrate, very slender, branched or not, frequently rooting at the nodes, pubescent with minute stellate and long simple hairs. *Leaves* with the petiole slender, usually shorter than the blade, 0.5-3.5 cm long, pubescent with minute stellate and long simple hairs, the stipules small and subulate; blade ovate to broadly ovate, very asymmetric, deeply cordate at the base, more or less obtuse to acute or acuminate at the apex, serrate or crenate at the margin, up to 5.5 cm long and 4 cm broad, membranous, usually 7-palminerved, sparsely hirsute with mostly simple hairs and with the main veins prominulous on both surfaces. *Flowers* axillary, solitary, the pedicel short to elongate and up to 2 cm long, filiform, articulated above the middle, sparsely to densely pubescent with minute stellate and longer simple hairs; calyx pyramidal, 5-plicate-angulate, 5-6 mm long, membranous, pubescent, greatly accrescent and up to 8 mm in fruit, the lobes broadly trullate, overlapping at the base, acuminate at the apex, 3-5 mm long, ciliate at the margins; petals broadly obovate-cuneate, truncate or subretuse at the apex, slightly shorter to slightly longer than the calyx, 5-7 mm long and 4-5 mm wide, yellow or whitish; staminal tube ca 2.5 mm long, glabrous, the filaments ca 1-2 mm long. *Mericarps* 5, ca 2 mm long, thin-walled, muticous or nearly so at the apex, dorsally reticulate, glabrous or sparsely papillate.

Mexico to Argentina; moist thickets.

CANAL ZONE: Balboa, *Standley 27169* (US), *32116* (US). COCLÉ: mountains beyond La Pintada, alt 400-600 m, *Hunter & Allen 513* (F, MO); vic of El Valle, alt 600-1000 m, *Allen 1168* (F, MO, US). PANAMA: Las Sabanas, *Bro. Heriberto 271* (F, US); Bella Vista, *Standley 25326* (US); vic of Juan Franco Race Track, nr Panama City, *Standley 27705* (US); nr Matías Hernández, *Standley 28946* (US).

3. SIDA LINIFOLIA Cav., Mon. Cl. Diss. Dec. 14, *t. 2(1)*. 1785.

Herb, annual or biennial, the stem erect, simple or more or less branched above, up to more than 1 m high, the branches suberect, pubescent with simple and/or stellate hairs. *Leaves* short-petiolate, the petiole 3-10 mm long, pilose, the stipules filiform to narrowly lanceolate, 4-7 mm long, pilose; blade linear or narrowly lanceolate, rounded or truncate or infrequently shallowly subcordate at the base, acute at the apex, entire-margined, 2-14 cm long and 2-15 mm broad, 3-nerved from the base, pubescent with simple and/or stellate hairs, the indumentum usually denser beneath, the main veins prominulous beneath. *Inflorescences* terminal, corymbiform or short-racemose, 8- to 20-flowered. *Flowers* with the pedicel 6-15 mm long, articulated 2-3 mm below the apex, hirtellous; calyx campanulate, subterete, 4.8-7 mm long, hirtellous to hirsute, persistent, the lobes triangular, acute, ca 2-4 mm long and 2.5-3 mm broad at the base; petals obovate, 8-15 mm long and 4-5 mm wide, cream-colored or whitish, usually with a maroon or dark purple center; staminal tube ca 2-3 mm long, minutely hyaline-puberulus near the apex, the filaments 0.5-1.0 mm long; styles 5-6 mm long, connate basally. *Mericarps* (5-)7-9, trigonous, shortly 2-apiculate, 2.5-3.5 mm long, papyraceous, dull, brownish-black, glabrous, the lateral walls fragile and fragmenting at maturity; seeds ca 2 mm long, dull, dark brown, glabrous except for a few minute hairs around the hilum.

Tropical America and tropical Africa; dry savannas, brushy and grassy slopes, grassy fields.

CANAL ZONE: along drowned Río Azote Caballo, alt 66-70 m, *Dodge et al. 16829* (MO); along the old Las Cruces Trail, between Fort Clayton and Corozal, *Standley 29161* (US); Corozal, *Standley 27363* (US); Cerro Ancon, *J. M. & M. T. Greenman 5118* (MO), *Bro. Heriberto 60* (US), *Standley 25170* (US), *26320* (US). CHIRIQUÍ: Boquete, elev 4000 ft, *M. E. Davidson 752* (F); vic of Boquete, Llanos Francia, alt 3300 ft, *Stern et al. 1179* (MO, US). COCLÉ: Penonomé and vic, *R. S. Williams 180* (US). PANAMA: Nueva Gorgona, *Duke 4542* (MO); along road toward top of Cerro Campana, *Duke 6015* (MO); Cerro Campana, *Ebinger 911* (MO); N of Panama City, *Bro. Paul 550* (US); vic of Juan Franco Race Track, *Standley 27824* (US); nr Punta Paitilla, *Standley 26298* (US); Las Sabanas, *Bro. Heriberto 144* (US); between Las Sabanas and Matías Hernández, *Standley 31867* (US); Río Tapía, *Standley 28177* (US); Río Tocumen, *Standley 29478* (US); Pacora, *Killip 3280* (US); Laguna de Portala, nr Chepo, alt 50 m, *Pittier 4596* (US); nr Chepo, alt 30 m, *Hunter & Allen 32* (F, MO, US); Taboga Island, alt 0-250 m, *Pittier 3595* (US); San José Island, *Erlanson 288* (GH, US), *Johnston 927* (GH, MO, US), *946A* (GH), *1162* (GH), *1182* (GH), *1213* (GH, MO).

4. SIDA QUINQUENERVIA Duchassaing ex Triana & Planchon, Ann. Sci. Nat., Bot., sér. 4, **17:** 176. 1862.

S. guianensis K. Schum. in Mart., Fl. Bras. **12**(3): 305. 1891.
Sidastrum quinquenervium (Duchassaing ex Triana & Planchon) Baker f., J. Bot. **30:** 137. 1892.

Herb or suffrutex up to 1.2 m high, the stem unbranched or sparingly branched above, copiously fulvous-stellate-hirsute. *Leaves* short-petiolate, the petiole up to 1.5 cm long, densely fulvous-stellate-hirsute, the stipules subulate; blade ovate to narrowly ovate or narrowly oblong-ovate, truncate, rounded or subcordate at the base, acute to acuminate at the apex, crenate to serrate at the margin, up to 10 cm long and 4.5 cm broad, 3- to 5-palminerved, scabridulous on both surfaces, stellate-pubescent above, more or less densely stellate-puberulus beneath, the venation prominent on the lower surface. *Flowers* in dense, axillary clusters, and in spike-like, terminal inflorescences, the individual flowers subsessile, subtended by several subulate, stellate-hirsute bracts longer than the calyx, the flowers thus appearing involucellate; calyx campanulate, 5-gonous, lobed to about the middle, 6-7 mm long, densely fulvous-stellate-hirsute, moderately accrescent, the lobes broadly triangular, acute, ca 3.5 mm long and 4.5 mm wide at the base; petals obovate, strongly oblique, unguiculate, emarginate at the apex, 8-9 mm long, yellow, the claw densely whitish-stellate-tomentellous; androecium 5-6 mm long, the staminal tube 3-4 mm long, whitish-stellate-puberulus; styles up to 8 mm long, connate basally. *Mericarps* 7-10, trigonous, muticous or apiculate (?), dorsally convex, 2-2.5 mm long, membranous, smooth, sparsely stellate-puberulus at the apex, dehiscent to the base dorsally; seeds trigonous, ca 1.8 mm long, sparsely puberulus.

Panama, Guiana and Brazil; wet thickets.

CANAL ZONE: hills W of the Canal, nr Gatun, *Standley 27298* (US). PANAMA: prob. nr Panama City, *Duchassaing s.n.* (type, fragment F, photo MO, US).

5. SIDA ACUTA Burm. f., Fl. Ind. 147. 1768.

S. ulmifolia Mill., Gard. Dict. ed. 8. 1768.
S. carpinifolia L. f., Suppl. Pl. Syst. Veg. 307. 1781.
S. acuta var. *carpinifolia* (L. f.) K. Schum. in Mart., Fl. Bras. **12**(3): 326. 1891.

Herb, suffrutex or shrub, perennial, erect, seldom spreading, 0.2-1.8 m high, usually much branched mostly from the base, glabrescent or sparsely pubescent with short stellate and/or long simple hairs, seldom copiously pubescent. *Leaves* distichous, short-petiolate, the petiole 2.5-8 mm long, the stipules conspicuous, narrowly ovate to linear, 7-15 mm long, usually 3-nerved, persistent; blade ovate to narrowly oblong-ovate, sometimes more or less ovate or elliptic or even somewhat rhombic, more or less asymmetric, obtuse to rounded at the base, acute at the apex, finely to coarsely serrate or dentate-serrate at the margin, rarely crenate, variously sized, 1.5-10 cm long and 0.8-3.5 cm broad, 3(-5)-palminerved, green on both sides, minutely stellate-puberulus and/or with scattered, rather long and mostly simple whitish hairs, or glabrescent, the venation slightly prominent beneath. *Flowers* axillary, solitary or in small, pseudo-umbellate inflorescences, the pedicel slender, articulated generally below the middle, 2-12 mm long; calyx broadly campanulate, subplicate-5-angulate, 6-9 mm long, foliaceous, 10-ribbed, sparsely to densely hirsute on margins and veins, and/or sometimes minutely stellate-puberulus, or nearly glabrous, moderately accrescent, the lobes broadly triangular, gradually acuminate, ca 3-5.5 mm long and 3-4.8 mm broad, infrequently shallowly triangular, caudate-cuspidate, ca 2.5-3.5 mm long and 5-7 mm broad, the cusp ca 1-1.5 mm long; petals broadly obovate-cuneate, strongly oblique, subretuse at the apex, 8-10 mm long and 6-8.5 mm broad, yellow, infrequently white; androecium 5-6 mm long, the staminal tube ca 3-4 mm long, minutely stellate-puberulus, rarely glabrous, the filaments numerous, ca 2 mm long; styles filiform, 5-5.5 mm long, connate at the base for ca 1-2 mm. *Mericarps* 7-9(-12), triquetrous, 2.5-4 mm long, chartaceous, the dorsum with the lower part rugose-reticulate and glabrous, and with the upper part minutely puberulus and with 2 longitudinal, low crests, each terminating into a short beak up to 0.8 mm long, the lateral walls more or less reticulate; seeds trigonous, ca 2-2.5 mm long, puberulus around the hilum.

A weedy, polymorphic plant, widely distributed in tropical and subtropical regions of both hemispheres; savannas, fields, waste ground and moist thickets. The fibers of the stem of the *escobilla* are used for making cordage, and bundles of the tough branches serve generally in place of ordinary brooms and brushes.

The species is represented in Panama by two varieties characterized as follows:

a. Calyx lobes broadly triangular, gradually acuminate, ca 3-4 mm long and 3-3.5 mm broad; staminal tube minutely stellate-puberulus ....var. ACUTA

aa. Calyx lobes shallowly triangular, caudate-cuspidate, ca 2.5-3.5 mm long and 5-7 mm broad, the cusp ca 1-1.5 mm long; staminal tube glabrous ....var. CUSPIDATA

5a. SIDA ACUTA var. ACUTA.

BOCAS DEL TORO: Water Valley, *von Wedel 769* (MO); Little Bocas, vic of Chiriquí Lagoon, *von Wedel 2543* (MO, US); s. loc., *von Wedel 214* (MO). CANAL ZONE: nr old Fort Lorenzo, mouth of Río Chagres, *Piper 5980* (US); nr Fort Randolph, *Maxon & Harvey 6546* (US); hills W of the Canal, nr Gatun, *Standley 27296* (US); Barro Colorado Island, *Shattuck 482* (F, MO), *539* (F); Frijoles, *Ebinger 81* (MO), *Standley 27635* (US); Gamboa, *Standley 28479* (US); Empire to Mandinga, *Piper 5499* (US); around Tabernilla, alt 20-25

m, *Pittier 3818* (US), *3819* (US); Summit, *Standley 26924* (US); Las Cascadas Plantation, nr Summit, *Standley 29528* (US); Balboa, *Macbride & Featherstone 40* (F, MO, US), *Standley 25505* (US). CHIRIQUÍ: Cerro de la Plata, nr San Felix, alt 120-150 m, *Pittier 5169* (US); vic of Puerto Armuelles, alt 0-75 m, *Woodson & Schery 826* (MO, US); vic of Boquete, alt 1200-1500 m, *Woodson & Schery 714* (MO); 3 mi S of El Volcán, elev 4000 ft, *Tyson 893* (MO). COLÓN: Colón, *Macbride & Featherstone 4* (F, US), *Rose 23999* (US). DARIEN: vic of Paya, Río Paya, *Stern et al. 258* (MO). PANAMA: Río Potrero, ca 2 mi from Arraijan, *Duke 4678* (MO); Las Sabanas, N of Panama City, *Bro. Paul 592* (US); vic of El Llano, *Duke 5859* (MO); Río Canita, along Pan-Am. Highway, nr Jenine, *Duke 3883* (MO), *3902* (MO); Taboga Island, *Standley 27065* (US), *Woodson et al. 1452* (MO); San José Island, *Erlanson 127* (GH), *347* (GH, US), *Johnston 897* (GH), *1083* (GH). PROVINCE UNKNOWN: *Stork 144* (US).

5b. SIDA ACUTA var. **CUSPIDATA** A. Robyns, var. nov.

A var. *acuta* calycis lobis depresse triangularibus caudato-cuspidatis ca 2.5-3.5 mm longis 5-7 mm latis et cuspidi ca 1-1.5 mm longa tuboque stamineo glabro distincta.

Probably throughout the range of the species in the New World.

COCLÉ: Aguadulce, nr sea level, *Pittier 4835* (US). PANAMA: Las Sabanas, N of Panama City, *Bro. Paul 509* (US); Cerro Azul, *Dwyer 3084* (holotype MO); Taboga Island, *Pittier 3623* (US), *Standley 27050* (US).

6. SIDA PYRAMIDATA Cav., Mon. Cl. Diss. Dec. 11, *t. 1(10)*. 1785, *t. 194(1)*. 1788.

Herb or small shrub up to 2.5 m high, the stem erect, branched above, rather copiously puberulus with very minute stellate hairs. *Leaves* long-petiolate, the petiole slender, up to 11.5 cm long, very minutely stellate-puberulus, the stipules subulate and up to 1 cm long; blade broadly ovate, truncate, rounded or shallowly cordate with a very open sinus at the base, long-acuminate at the apex, crenate or serrate at the margin, up to 12 cm long and 10 cm broad, 5- or 7-palminerved, slightly discolor, sparsely and minutely stellate-puberulus above, paler, rather densely and minutely stellate-puberulus, and with the venation prominent beneath, the indumentum always denser when young, the uppermost leaves much reduced. *Flowers* in small, dense glomerules disposed in large, open, long-branched, terminal, leafy panicles, these becoming short-branched and nearly leafless toward the apex, the individual flowers shortly pedicellate; calyx globose-campanulate, terete, 3.5-4 mm long, minutely stellate-puberulus, persistent, the lobes deltoid, acuminate, 1.8-2.5 mm long and 1.8-2.2 mm broad at the base; petals obovate, strongly oblique, unguiculate, emarginate at the apex, 5-6(-8) mm long and 2.2-3 mm broad, yellow or orange, the claw sometimes reddish and minutely stellate-tomentellous; androecium ca 3.5-4 mm long, the staminal tube ca 2-2.5 mm long, sparsely and minutely stellate-puberulus; styles 3.5-4 mm long, connate basally for ca 2 mm. *Mericarps* 5-7(-8), trigonous, dorsally convex and inconspicuously 1-veined longitudinally, usually shortly 2-rostrate at the apex, 1.7-3 mm long, rigid-chartaceous, densely and minutely stellate-puberulus except at the base, the beaks ca 0.5-0.9 mm long; seeds trigonous-subrotund, 1-1.5 mm long and broad, glabrous.

West Indies and Mexico to Colombia and Venezuela; moist thickets.

CANAL ZONE: vic of Gatuncillo, *Piper 5658* (US); along an old trail above the Reservoir, 1-3 mi from Gorgona, alt 40-150 m, *Maxon 4740* (US); Obispo, *Standley 31737* (US); Empire to Mandinga, *Piper 5454* (US), *5522* (US); Albrook, *Dwyer & A. Robyns 31* (MO); Ancon Hill, elev 600 ft, *R. S. Williams 20* (US). PANAMA: Alahajuela, *Woodworth & Vestal 734* (F); Panama City (?), *Hayes s.n.* (US); vic of Bella Vista, *Piper 5351* (US).

7. SIDA SETIFERA Presl, Rel. Haenk. **2:** 105. 1835.

? *S. aggregata* Presl, loc. cit. 106.

Herb or slender shrub up to 1.8 m high, much branched, finely stellate-tomentellous and generally also with patent, yellowish hairs to 3 mm long. *Leaves* long-petiolate, the petiole up to 7 cm long, minutely stellate-tomentellous and long-hirsute, the stipules linear-subulate, 4-7 mm long, deciduous; blade ovate to broadly ovate, cordate at the base, acute to subacuminate at the apex, crenate, serrate or dentate at the margin, 3-10 cm long and 2-7 cm broad, smaller toward the apex of the branches, slightly discolor, 7- or 9-palminerved, densely stellate-tomentellous on both sides when young, becoming stellate-puberulus, pale and prominently veined beneath. *Flowers* mostly in axillary, dense, several-flowered glomerules toward the apex of the leafy branches or branchlets (or sometimes terminal?), often simulating spike-like or racemiform inflorescences, the individual flowers subsessile or very short-pedicellate; calyx cupuliform, 5-angled, ca 7 mm long, stellate-tomentellous and densely long-hirsute, moderately accrescent, the lobes triangular, acute, ca 4.5-5 mm long and 3.5 mm broad at the base; petals broadly obovate-cuneate, inconspicuously oblique, more or less undulate at the apex, 7.5-8 mm long and ca 7 mm broad, yellow or orange with a maroon or reddish center; androecium ca 5-5.5 mm long, the staminal tube rather broad, ca 4 mm long and 1 mm in diam, sparsely and minutely hispidulous, the filaments numerous; styles 4.5-5.5 mm long, connate basally for ca 1-1.5 mm. *Mericarps* (5)6-8, trigonous, more or less muticous to acute at the apex, ca 2-2.3 mm long, pergameneous, minutely tomentellous toward the apex dorsally, the dorsum 1-veined longitudinally and finely striate-reticulate, the lateral walls nearly smooth, dehiscent apically; seeds trigonous, ca 1.5-1.7 mm long, glabrous or with few very minute hairs around the hilum.

West Indies and Mexico to northern South America; moist thickets. On San José Island (cf. Johnston, Sargentia **8:** 197. 1949) it grows "abundantly in disturbed places," and "occasional in second growth along roads and trails through low thickets."

PANAMA: Tumba Muerto road, nr Panama City, *Standley 29764* (US); Taboga Island, *Bro. Celestine* 42 (US); San José Island, *Johnston 979* (GH), *1282* (GH, MO).

According to Standley (Contr. U. S. Nat. Herb. **27:** 254. 1928, under *S. aggregata*), it is "of infrequent occurrence, on the Pacific slope" of the Canal Zone.

8. SIDA RHOMBIFOLIA L., Sp. Pl. 684. 1753.

Herb or shrub up to 1.5 m high, the stem erect, usually profusely branched, minutely stellate-puberulus, infrequently also hirsute with mostly simple hairs, ultimately glabrescent. *Leaves* short-petiolate, the petiole usually ca 5 mm long,

more or less densely stellate-puberulus and sometimes also hirsute, the stipules subulate, 5-10 mm long, more or less persistent; blade often more or less rhombic, narrowly ovate, narrowly oblong-elliptic, or narrowly oblong-obovate, cuneate to obtuse at the base, obtuse or acute at the apex, serrate or serrulate above the base at the margin, varying much in size, 1.5-8.5 cm long or sometimes shorter and 0.6-3.5 cm broad, 3(-5)-palminerved, discolor, shortly and sparsely stellate-puberulus or almost glabrous on the dark green upper surface, more or less densely and minutely stellate-puberulus to stellate-tomentellous and infrequently also hirsute especially along the main veins on the pale lower surface, the main veins prominent beneath. *Flowers* axillary and solitary, those toward the apex of the branches and branchlets often corymbose, the pedicel short to usually elongate and up to 3.5 cm long, filiform, articulated generally above the middle, minutely stellate-puberulus and sometimes also hirsute, the fruiting pedicel slightly longer; calyx campanulate, subplicate-5-angulate, ca 6(9) mm long, foliaceous, green, with the 5 midribs and 5 commissural ribs markedly thickened and yellowish at the base, minutely stellate-tomentellous, sometimes also hirsute especially on the ribs and along the margins, moderately accrescent, the lobes deltoid, acuminate, ca 3(5) mm long and broad at the base; petals broadly ovate, strongly oblique, unguiculate, slightly emarginate at the apex, 7-8.5(15) mm long and 5-6(13) mm wide, yellow or sometimes orange or white, the claw minutely tomentellous; androecium ca 5.5(9) mm long, the staminal tube ca 3.5(6) mm long, sparsely and minutely stellate-puberulus; styles ca 4(8) mm long, connate basally for ca ½ of their length or less. *Mericarps* (7)8-12(14), triquetrous, 2.2-5.5 mm long (the beaks included), chartaceous, the dorsum with the lower part rugose-reticulate, and with the upper part with 2 longitudinal crests, each terminating into a beak 0.2-2.5 mm long, the lateral walls more or less rugose-reticulate, glabrous or with very minute stellate hairs on crests and beaks; seeds trigonous-subrotund, ca 2 mm long, smooth, glabrous but minutely whitish-pilose near the hilum.

A polymorphic, widely distributed weed in tropical and subtropical regions of both hemispheres; savannas, roadsides, moist thickets, brushy fields and slopes, wooded swamps, and gravel bars; known in Panama as *escobilla* or *hierba de puerco;* according to Standley (Contr. U. S. Nat. Herb. **27:** 254. 1928), it "is a plant to be avoided if one does not like ticks."

BOCAS DEL TORO: region of Almirante, research grounds, *Cooper 85* (F). CANAL ZONE: Chagres, *Fendler 13* (MO, US), *14* (MO, US), *18* (MO, US); vic of Fort Sherman, *Standley 30990* (US); Gatun, *Bro. Heriberto 119* (US); hills W of the Canal, nr Gatun, *Standley 27297* (US); Barro Colorado Island, *Ebinger 226* (MO); vic of Frijoles, *Piper 5780* (US); Navy Reservation, N of Gamboa, *A. Robyns 65-57* (MO); Empire to Mandinga, *Piper 5503* (US); Summit, *Standley 26919* (US); around Culebra, alt 50-150 m, *Pittier 2219* (US); hills E of Curundu, *Harvey 5205* (F); Albrook, *Dwyer & A. Robyns 179* (MO); Ancon Hill, *J. M. & M. T. Greenman 5013* (MO), *5121* (MO); Balboa, *Standley 32132* (US); hills between Río Grande and Pedro Vidal, on road to Arraijan, alt 50-150, *Pittier 2713* (US). CHIRIQUÍ: trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, alt 1500-2000 m, *Allen 1509* (F, MO, US); Finca Lérida to Boquete, alt ca 1300-1700 m, *Woodson et al. 1136* (F, MO). COCLÉ: Aguadulce, nr sea level, *Pittier 4885a* (US); El Valle de Antón, trails nr Finca Tomas Arias, alt 600 m, *Allen 4231* (MO). COLÓN: between France Field, Canal Zone, and Catival, *Standley 30209* (US); Portobello, *Ebinger 120* (MO). DARIEN: headwaters Río Chico, alt 500-700 ft, *Allen 4618* (MO). HERRERA: Ocú,

Ebinger 1074 (MO). PANAMA: Las Sabanas, N of Panama City, *Bro. Paul 573* (US); Bella Vista, *Standley 25394* (US); nr Matías Hernández, *Standley 28896* (US); between Matías Hernández and Juan Díaz, *Standley 32087* (US); vic of El Llano, *Duke 5800* (MO); Las Delicias, *Carleton 46* (US); San José Island, *Johnston 811* (GH), *836* (GH). SAN BLAS: forests around Puerto Obaldía, alt 0-50 m, *Pittier 4381* (US), *4382* (US). PROVINCE UNKNOWN: *Stork 151* (US).

The collection *Allen 1509* (Chiriquí), with exceptionally large flowers—calyx ca 9 mm long, petals ca 15 mm long and 13 mm broad, androecium ca 9 mm long, and styles ca 8 mm long—can, perhaps, be considered as a distinct variety.

9. SIDA PANICULATA L., Syst. Nat. ed. 10, 1145. 1759.

Herb or suffrutex, perennial, up to 1 m high or more, the stem erect, branched, more or less densely fulvous-stellate-pubescent, at length glabrescent. *Leaves* very short- (upper leaves) to rather long-petiolate (lowest ones), the petiole up to 9 cm long, stellate-tomentose or stellate-villous, the stipules subulate, 5-8 mm long; blade broadly to narrowly ovate, cordate at the base, acute to short-acuminate at the apex, crenate or serrate at the margin, varying much in size, 5-15 cm long and 3-7 cm broad, smaller toward the apex of the branches and branchlets, 5- or 7(-9)-palminerved, the upper surface sparsely and minutely stellate-puberulus, the lower one stellate-tomentose, the indumentum always much denser when young, the main veins impressed above and prominulous beneath. *Flowers* small, very numerous, solitary and axillary, usually with an accessory flowering branchlet arising later from the same axil, ultimately forming altogether more or less open paniculiform inflorescences, the flowering branchlets racemose and slender, the pedicels capillaceous, articulated above the middle, 1.5-4 cm long, with few, minute stellate hairs or glabrous; calyx campanulate, terete, 2.7-3.5 mm long, more or less densely and minutely stellate-puberulus, moderately accrescent, the lobes deltoid, acute, ca 1.3-2 mm long and 1.1-1.8 mm broad at the base; petals reflexed, spatulate or obovate, slightly oblique, unguiculate, retuse at the apex, 3.5-5 mm long and 1.5-3 mm broad, crimson or purple; androecium 4-7 mm long, the staminal tube 2-4 mm long, minutely stellate-puberulus; styles 6-8 mm long, connate basally. *Mericarps* 5, trigonous, 2.5-4 mm long, chartaceous, acute or shortly 2-aristate and with the beaks close together at the apex, the dorsum convex, more or less rugose especially below, and minutely stellate-puberulus especially above, the lateral walls reticulate; seeds trigonous-subrotund, ca 1.5-1.7 mm long, with scattered minute hairs, these denser around the hilum.

West Indies and southern Texas to northern Argentina; tropical Africa.

This species was reported by Hemsley (Biol. Centr.-Am. **1:** 106. 1879) to have been collected in Panama by Sutton Hayes (287?).

10. SIDA GLOMERATA Cav., Mon. Cl. Diss. Dec. 18, *t.* 2(6). 1785.

Herb, often woody at the base, or suffrutex, perennial, the stem usually erect, up to 1.2 m high, branched, the younger parts with short stellate hairs and/or hirsute with simple or stellate hairs. *Leaves* distichous, short-petiolate, the petiole 5-7 mm long, tomentose, the stipules conspicuous, narrowly ovate, attenuate-

acuminate, 8-12 mm long and up to 4 mm wide, 3- to 5- to several-nerved, glabrous except the ciliate margins, persistent; blade narrowly ovate, often slightly asymmetric and obtuse or cuneate or slightly subcordate at the base, acute or acuminate at the apex, more or less unequally and rather sharply serrate, up to 7 cm long and 2.5 cm broad, usually 3- or sub-5-palminerved, appressed-hirsute with mostly simple hairs on both sides, the indumentum denser beneath, the venation prominulous on the lower surface. *Flowers* axillary, solitary or usually glomerate, subsessile to short-pedicellate; calyx campanulate, sharply 5-angulate, 5-7 mm long, 10-ribbed, with long white hairs especially on veins and along margins, moderately accrescent, the lobes deltoid, long-acuminate, 2.5-3.5 mm long; petals obtriangular, strongly oblique, retuse at the apex, ca 8 mm long, yellow or whitish; androecium ca 4-4.5 mm long, the staminal tube ca 2.5 mm long, glabrous or nearly so; styles ca 5 mm long, connate basally. *Mericarps* 5, trigonous, 2-2.5 mm long, chartaceous, glabrous, the dorsum with the lower part rugose-reticulate, and with the upper part with 2 longitudinal low crests, these obtuse and terminating each into a small apiculum, the lateral walls reticulate; seeds trigonous, ca 1.5-1.7 mm long, minutely puberulus only around the hilum.

West Indies and Central America to Brazil, Paraguay, and Bolivia; roadsides, cultivated land, savannas, brushy slopes, and coastal thickets. Like the closely related *S. acuta* it is known in Panama as *escobilla;* the tough branches are often used as rough brooms.

CANAL ZONE: Gatun, *Hayes s.n.* (287?) (MO, US); Obispo, *Standley 31667* (US); Empire to Mandinga, *Piper 5468* (US); Corozal, *Standley 27362* (US); hills E of Curundu, *Harvey 5204* (F); Ancon, *Bro. Celestine* 85 (US). CHIRIQUÍ: vic of Boquete, alt 1200-1500 m, *Woodson & Schery 713* (MO). DARIEN: s. loc., *Macbride 2698* (F, US). PANAMA: hills between Capira and Potrero, alt 80-130 m, *Dodge & Hunter 8615* (MO), *8627* (MO); Bella Vista, *Standley 25363* (US); Tumba Muerto, *Bro. Heriberto 179* (US); Taboga Island, *Standley 27987* (US).

11. Sida jamaicensis L., Syst. Nat. ed. 10, 1145. 1759.

Herb, woody below, or suffrutex, perennial, the stem often decumbent, up to 1 m long, the younger parts softly stellate-subtomentellous. *Leaves* distichous, short-petiolate, the petiole 4-7 mm long, stellate-subtomentellous, the stipules linear-subulate, equalling more or less the petiole, hirsute, at length caducous; blade broadly ovate to ovate, subrhombic or oblong, more or less oblique or obtuse at the base, acute or obtuse at the apex, serrate above the base at the margin, up to 4 cm long and 2.3 cm broad, nearly concolorous, 3- or 5-palminerved, the upper surface stellate-puberulus, the lower surface pale, stellate-tomentellous to densely stellate-puberulus, and with the primary and secondary veins prominent. *Flowers* solitary in the axils, often with another flower or a short flowering branch (this often very short, simulating a small glomerule) appearing later in the same axils, the pedicel short, 2-4 mm long, inarticulated, stellate-subtomentellous; calyx campanulate, subplicate-5-angulate, lobed to below the middle, 6-7.5 mm long, 10-ribbed, stellate-subtomentellous, moderately accrescent, the lobes triangular, gradually long-acuminate; petals obovate-cuneate, strongly oblique, 6-7 mm long and ca 4 mm broad, white; androecium 4.5-5 mm long, the staminal tube ca 3 mm

long, inconspicuously puberulus toward the apex; styles ca 5 mm long, connate halfway. *Mericarps* 5, trigonous, ca 2.5-3 mm long, pergameneous, the dorsum with the lower part rugose-reticulate and glabrous, and with the upper part minutely stellate-tomentellous and with 2 longitudinal low crests, each terminating into a short beak up to 0.8 mm long, the lateral walls fragile, reticulate; seeds trigonous, ca 1.5 mm long, minutely puberulus only around the hilum.

West Indies, southern Mexico (?), Guatemala, Panama, and northern South America.

COCLÉ: Aguadulce, in savannas, nr sea level, *Pittier 4885* (US). PANAMA: Bella Vista, coastal thicket, *Standley 25372* (US).

12. SIDA GLUTINOSA Cav., Mon. Cl. Diss. Dec. 16, *t.* 2(8). 1785.

Herb, sometimes suffrutex, perennial, the stem usually erect, up to 1.2 m high, puberulus with short viscid hairs and sparsely hirsute with longer simple hairs on the younger parts. *Leaves* with the petiole slender, usually 1.5-3.5 cm long, viscid-puberulus and hirsute, the stipules subulate, 1-2.5 mm long, persistent; blade ovate, cordate at the base, long-acuminate at the apex, irregularly serrate at the margin, up to 7.5 cm long and 3.5 cm broad, much reduced toward the apex of the stem and branchlets, thin, 5- or 7(-9-11)-palminerved, the main veins prominulous above and beneath, stellate-puberulus on both surfaces but the indumentum denser below. *Flowers* solitary in the axils, often with another flower or an accessory flowering branchlet arising later from the same axils, ultimately forming altogether a leafy paniculiform inflorescence, the pedicel short to usually elongate, filiform, articulated generally above the middle, 1-2.5 cm long, viscid-puberulus and sparsely hirsute; calyx campanulate, subplicate-5-angulate, 5-6.5 mm long, membranous, green, 10-ribbed, viscid-puberulus and/or hirsute along the veins and margins, moderately accrescent, the lobes deltoid, conspicuously acuminate, 3-3.5 mm long; petals obovate-obtriangular or broadly so, inconspicuously oblique, unguiculate, slightly emarginate at the apex, 5-6.5 mm long and 3-5 mm broad, yellow, buff or white; androecium 3.5-4.5 mm long, the staminal tube ca 2-3 mm long, sparsely whitish-hirtellous; styles ca 3.5-4 mm long, connate basally. *Mericarps* 5, trigonous, ca 3 mm long (awns included), thin-walled, puberulus toward the apex, apically 2-aristate, the awns 0.5-1.2 mm long and puberulus with antrorse or spreading hairs, the dorsum convex, nearly smooth as the lateral walls, dehiscent apically; seeds trigonous, ca 1.5 mm long, glabrous except for a few scattered minute hairs around the hilum.

West Indies and Mexico to Colombia and Venezuela; moist thickets and woods, clearings, and roadsides.

CANAL ZONE: vic of Gatuncillo, *Piper 5628* (US); Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, *Piper 5748* (US); hills between Río Grande and Pedro Vidal, on road to Arraijan, alt 50-150 m, *Pittier 2714* (US). PANAMA: Paitilla, *Bro. Heriberto 237* (F, US); vic of Juan Franco Race Track, nr Panama City, *Standley 27710* (US); nr Matías Hernández, *Standley 28882* (US); between Matías Hernández and Juan Díaz, *Standley 32042* (US); Río Tapia, *Standley 26202* (US); Río Tocumen, *Standley 29414* (US); nr the big swamp E of the Río Tocumen, *Standley 26585* (US).

13. Sida urens L., Syst. Nat. ed. 10, 1145. 1759.

Herb, sometimes suffrutex, the stem slender, usually erect, rarely procumbent, up to 2.5 m high, branched often from the base, rather sparsely hirsute with long, patent, mostly simple or sometimes few-armed, yellowish hairs, and often also with shorter stellate hairs. *Leaves* with the petiole 1.4-5 cm long, more or less densely hirsute, the stipules subulate, ca 3-4 mm long, hirsute, caducous; blade ovate, sometimes narrowly so, cordate at the base, gradually long-acuminate at the apex, serrate at the margin, up to 10 cm long and 5 cm broad, thin, nearly concolorous, 5- to 9(sub-11)-palminerved, more or less strigose-pubescent on both sides, the indumentum denser on the prominulous primary veins beneath, the hairs simple to few-armed or stellate. *Flowers* mostly in axillary or subterminal, few- to several-flowered glomerules, those toward the apex of the branches and branchlets often simulating spike-like inflorescences, the individual flowers subsessile to short-pedicellate; calyx campanulate, subplicate-5-angulate, ca 8 mm long, membranous, 10-ribbed, yellowish-hispid or subsetose on veins and along margins, moderately accrescent, the lobes broadly triangular, from the base gradually long-acuminate, ca 4.5-5 mm long and 4-4.5 mm broad at the base; petals broadly obovate-cuneate, oblique, sometimes inconspicuously so, usually emarginate at the apex, ca 7(9) mm long and 5(6) mm broad, pale buff, salmon, white or yellow, often reddish at the base, very minutely hyaline-puberulus at the claw; androecium ca 5 mm long, the staminal tube ca 2.5 mm long, sparsely hispidulous, the filaments relatively few; styles ca 4 mm long, connate basally. *Mericarps* 5, trigonous, 2-2.5 mm long, muticous to very shortly and bluntly 2-aristate at the apex, chartaceous, glabrous or somewhat puberulus near the apex, dorsally nearly smooth, laterally faintly striate, dehiscent apically; seeds trigonous, ca 1.5 mm long, glabrous but minutely puberulus around the hilum.

West Indies and southern Mexico to northern Argentina and Bolivia, and tropical Africa; moist thickets and woods, brushy slopes, grassy fields and roadsides. According to Standley (Contr. U. S. Nat. Herb. **27:** 254. 1928), "the hairs of the foliage are sufficiently stiff to penetrate the skin."

canal zone: Mount Hope Cemetery, *Standley 28805* (US); Gamboa, *Standley 28316* (US); Obispo, *Standley 31657* (US); between Summit and Gamboa, *J. M. & M. T. Greenman* 5259 (MO); Summit, *Standley 26912* (US); vic of Summit, *Standley 30127* (US), *30146* (US); Río Paraíso, above E Paraíso, *Standley 29885* (US); along the old Las Cruces Trail, between Fort Clayton and Corozal, *Hunter & Allen 745* (MO), *Standley 29195* (US); vic of Corozal, *Piper 5304* (US); Balboa, *Standley 29304* (US), *30884* (US). chiriquí Bajo Mono, elev 4500 ft, *M. E. Davidson 523* (F). panama: Las Sabanas, N of Panama City, *Bro. Paul 421* (US); along the Corozal Road, nr Panama City, *Standley 26815* (US); vic of Juan Franco Race Track, nr Panama City, *Standley 27696* (US); between Las Sabanas and Matías Hernández, *Standley 31926* (US); Río Tapía, *Standley 28077* (US); Taboga Island, *Standley 27073* (US), *27950* (US); San José Island, *Johnston 874* (GH, MO).

14. Sida glabra Mill., Gard. Dict. ed. 8. 1768.

S. ulmifolia Cav., Mon. Cl. Diss. Dec. 15, *t.* 2(4). 1785.
S. arguta Sw., Nov. Gen. Sp. Pl. Prodr. 101. 1788.

Herb or suffrutex, the stem erect or ascending or sprawling, up to 1.2 m long, the branches slender, rather sparsely and finely stellate-puberulus to glabrescent.

Leaves slender-petiolate, the petiole up to 4 cm long, flattened and hirsute on the adaxial side, rounded and nearly glabrous on the abaxial side, the stipules linear-subulate, 3-4 mm long, hirsute, persistent; blade broadly ovate, cordate at the base, acuminate at the apex, coarsely crenate-serrate at the margin, up to 3.2 cm long and 2.6 cm wide, thin, nearly concolorous, 5(-7)-palminerved, with both surfaces more or less sparsely strigose-pubescent, and with the venation prominulous. *Flowers* axillary, solitary, the pedicel capillaceous, obscurely articulated above the middle or inarticulated, 1.5-2.5 cm long, up to 4.5 cm long in fruit, finely stellate-puberulus especially above; calyx campanulate, subplicate-5-angulate, ca 5-5.5 mm long, thin, 10-ribbed, puberulus on the veins and ciliate at the margin, very moderately accrescent, the lobes deltoid, from the base long-acuminate, ca 2.5-3 mm long and broad at the base; petals ca 6-7 mm long, yellow. *Mericarps* 5, trigonous, narrow, ca 4 mm long (awns included), apically 2-aristate, the awns ca 1-1.5 mm long, very minutely antrorsely pilosulose as is the dorsal upper part, thin-walled, dorsally and laterally finely reticulate, dehiscent apically.

West Indies and Mexico to northern South America.

CANAL ZONE: in Government forest along Las Cruces Trail, alt 75 m, *Hunter & Allen 716* (MO).

This species is variable and not well understood. It is closely related and perhaps even conspecific with *S. veronicaefolia* Lam. (*S. humilis* Cav., *S. hederifolia* Cav., *S. dombeyana* DC.), which is widely distributed in the tropics of both hemispheres.

15. SIDA SPINOSA L., Sp. Pl. 683. 1753.

S. alba L., loc. cit. ed. 2, 960. 1763.
S. angustifolia Lam., Encycl. Méth. Bot. **1**: 4. 1783.

Herb or suffrutex, annual or perennial, the stem erect, up to 1.2 m high, slender and sparingly branched, densely and minutely stellate-puberulus, at length glabrescent. *Leaves* with the petiole slender, 3-15 mm long, sometimes with 2 more or less spinose, infrapetiolar callosities, minutely stellate-tomentellous, the stipules subulate-filiform, 4-6 mm long, hirtellous, at length caducous; blade polymorphic, lanceolate, linear-lanceolate or linear-oblong, seldom narrowly elliptic, rounded or truncate or infrequently shallowly subcordate at the base, acute or obtuse at the apex, crenate-serrate at the margin, 2-6 cm long and 0.3-1.8 cm broad, markedly discolor, 3- or 5-palminerved, the upper surface dark green (brownish when dry), minutely stellate-puberulus, and with the venation impressed, the lower surface pale, minutely and softly stellate-tomentellous, and with the venation prominent. *Flowers* axillary, solitary, often with a very short accessory flowering branchlet in the same axil, the flowers toward the apex of the branches and branchlets subcorymbose, the pedicel slender, articulated mostly above the middle, 2-9 mm long, minutely stellate-tomentellous; calyx cupuliform, 5-angulate, ca 5-5.5 mm long, 10-ribbed, minutely stellate-tomentellous, very moderately accrescent, the lobes deltoid, acute to acuminate, ca 2-2.5 mm long and broad at the base; petals strongly oblique, ca 6-7 mm long, orange (or yellow?); androecium ca 3.5-4 mm long, the staminal tube ca 3 mm long, minutely pilosulose, the filaments relatively few;

styles ca 3.5-4 mm long, connate basally. *Mericarps* 5, trigonous, ca 2.5 mm long, shortly 2-aristate at the apex, the awns ca 0.5-0.8 mm long, antrorsely pilosulose as is the dorsal upper part, the dorsal lower part membranous, the lateral walls membranous-chartaceous and striate-reticulate, apically dehiscent but the seed escaping thru the disintegrated base; seeds trigonous, ca 1.5 mm long, glabrous.

Widely distributed in tropical and subtropical regions of both hemispheres; savannas, moist thickets, brushy and grassy slopes and fields.

The Panamanian collections can be referred to the var. *angustifolia* (Lam.) Triana & Planchon, Ann. Sci. Nat., Bot., sér. 4, **17:** 172. 1862.

CANAL ZONE: along the old Las Cruces Trail, between Fort Clayton and Corozal, *Standley 29230* (US); Sosa Hill, Balboa, *Standley 25240* (US), *26421* (US). PANAMA: Las Sabanas, *Standley 25891* (US); Tumba Muerto Road, nr Panama City, *Standley 29820* (US); nr Matías Hernández, *Standley 28885* (US), *28890* (US); nr the big swamp E of the Río Tocumen, *Standley 26601* (US); San José Island, *Johnston 1061A* (GH).

16. Sida linearifolia St.-Hil. *et al.*, Fl. Bras. Merid. **1:** 180. 1827.

Herb, woody at the base, the stem erect, 60-90 cm high, simple or sparingly branched, stellate-subtomentose toward the apex. *Leaves* short-petiolate, the petiole 3-5 mm long, stellate-subtomentose, the stipules conspicuous, narrowly triangular, long-acuminate, about twice as long as the petiole, 7-8(-12) mm long and 1(-2) mm broad at the base, usually 3-nerved, ciliate at the margin, persistent even after the fall of the leaves; blade narrowly elliptic-rhombic to narrowly oblong, more or less rounded to subcordate at the base, acute at the apex, serrulate above the middle along the margin, 1.5-3.5 cm long and 3.5-10 mm broad, discolor, 3- or sub-5-palminerved, the upper surface green, sparsely pilose, at length glabrate, the lower surface pale, minutely stellate-tomentellous to densely stellate-puberulus, and with the main veins prominent. *Flowers* axillary and mostly solitary, sometimes with a short accessory flowering branchlet in the same axil, the flowers toward the apex of the branches and branchlets subcorymbose, the pedicel terete, articulated above the middle, usually elongate and up to 1.7 cm long, densely and very minutely stellate-puberulus; calyx campanulate, subplicate-5-angulate, lobed to about the middle, ca 7 mm long, foliaceous, green, with the 5 midribs and 5 commissural ribs markedly thickened and yellowish at the base, very minutely puberulus, hirsute on the ribs and along the margins, persistent, the lobes broadly triangular, from the base long-acuminate; petals broadly obovate-cuneate, oblique, truncate at the apex, ca 7-8 mm long, white with usually a dark purple basal spot; androecium ca 4 mm long, the staminal tube ca 2 mm long, inconspicuously pilosulose, the filaments few; styles ca 3-3.5 mm long, connate halfway. *Mericarps* 5, trigonous, ca 2.5 mm long, chartaceous, glabrous, shortly 2-rostrate at the apex, dorsally and laterally more or less rugose-reticulate, apically dehiscent; seeds trigonous, ca 1.7-1.8 mm long, inconspicuously puberulus around the hilum.

Panama and Brazil.

CANAL ZONE: Sosa Hill, Balboa, brushy slope, *Standley 26448* (US). PANAMA: Laguna de Portala, nr Chepo, alt 50 m, *Pittier 4586* (US).

These are the first collections reported for *S. linearifolia* in Panama as well as in North America.

14. WISSADULA Medic.

WISSADULA Medic., Malv.-Fam. 24. 1787.

Herbs, undershrubs or shrubs, the indumentum usually of stellate hairs. *Leaves* petiolate, the stipules caducous, the blade cordate or truncate at the base, the margins entire or dentate. *Flowers* axillary and solitary, or in terminal, paniculiform inflorescences; epicalyx wanting; calyx 5-merous, campanulate or somewhat turbinate, lobed to about or to below the middle, persistent; corolla small or medium-sized, the petals 5, the base adnate to the staminal tube; staminal tube short, ventricose, filamentiferous at the apex, the filaments relatively numerous, the anthers reniform; ovary of 5, rarely 3-4 or 6 carpels, each carpel (1)3-ovulate, the ovules anatropous, pendulous; styles isomerous with the carpels, the stigmas capitate. *Fruits* more or less stellate-turbinate or globose, of 5, rarely 3-4 or 6 mericarps, these angulate to rostrate apically and with the beaks pointing outwards, more or less completely divided into 2 superposed cavities by tranversal or oblique constriction of the lateral walls, the lower cavity 1-seeded, the upper with 2 collateral seeds, ultimately incompletely 2-valvate; seeds subglobose-reniform, pubescent; embryo curved, the albumen scant; cotyledons plicate.

A genus of some 40 species, predominantly American, but with a few species (perhaps only 1) known in the Old World tropics. It was monographed by Fries in 1908 (K. Sv. Vetenskapsakad. Handl. [ser. 4] **43**(4): 1-95).

The range of the genus in America is from southern Texas and the West Indies to Argentina. Three species occur in Panama.

a. Leaf blades narrowly triangular to triangular; pedicels elongate, filiform, up to 5 cm long .... 1. W. PERIPLOCIFOLIA

aa. Leaf blades narrowly to broadly ovate or oblong-ovate.

- b. Leaf blades ovate to broadly ovate, deeply cordate and with the basal lobes often overlapping, velvety on both sides, the lower surface densely whitish-stellate-tomentellous; pedicels 0.5-2.5 cm long, to 3.5 cm long in fruit .... 2. W. AMPLISSIMA
- bb. Leaf blades ovate or oblong-ovate, sometimes narrowly so, rounded or truncate or shallowly cordate with a very open sinus at the base, scabridulous above, the lower surface with 2 tiers of stellate hairs, the lower tier minutely whitish- or canescent-tomentellous, the upper one ferruginous-pubescent with longer, stellate hairs; pedicels 0.5-1 cm long or shorter, slightly longer in fruit .... 3. W. EXCELSIOR

1. WISSADULA PERIPLOCIFOLIA (L.) Presl, Rel. Haenk. **2**: 117. 1835.

Sida periplocifolia L., Sp. Pl. 684. 1753.

Herb or suffrutex, the stem erect, to 1.2 m high, the branches elongate, slender, more or less minutely stellate-tomentellous when young. *Leaves* with the petiole much shorter than the blade, 0.3-5 cm long, minutely stellate-tomentellous, the stipules very small, subulate, 1.5-3 mm long, early caducous; blade narrowly triangular to triangular, truncate to shallowly cordate with a very open sinus at the base, obtuse and inconspicuously mucronulate at the apex, entire-margined, up to 14 cm long and 6 cm broad, gradually smaller toward the apex, chartaceous, conspicuously discolor, usually 5-palminerved, the upper surface green or dark green

and more or less densely and minutely stellate-puberulus, the lower surface pale, minutely and softly stellate-tomentellous and with the venation prominent. *Flowers* axillary and solitary, forming very open, terminal, paniculiform inflorescences, the pedicels elongate, filiform, articulated above the middle, up to 5 cm long, more or less densely puberulus with minute, simple (and somewhat glandular?) and/or stellate hairs especially toward the apex; calyx campanulate-turbinate, lobed mostly to slightly below the middle, ca 2.5-3 mm long, more or less densely puberulus with minute, simple or stellate hairs, the lobes deltoid, acute, ca 1.5-2 mm long and broad at the base; petals broadly obovate-cuneate, ca 5 mm long and 3 mm broad, pale buff or pale yellow, the claw minutely ciliolate; androecium ca 2.5 mm long, the staminal tube only ca 1 mm long; styles ca 4 mm long, connate basally. *Fruit* turbinate, 5-lobed, constricted below the middle, the mericarps 5, 5-7 mm long, minutely puberulus especially above, apiculate and with the apiculum ca 0.5-1 mm long; seeds 3, reniform-subglobose, ca 1.5-2 mm in diam, more or less densely whitish-puberulus, the indumentum of the lower seed denser than that of the 2 upper seeds.

West Indies and southern Mexico to Brazil; moist thickets, wet forest, and brushy slopes.

The Panamanian collection can be referred to the var. *antillarum* R. E. Fries, K. Sv. Vetenskapsakad. Handl. [ser. 4] **43**(4): 34. 1908.

CANAL ZONE: in Government forest along Las Cruces Trail, alt 75 m, *Hunter & Allen 757a* (MO); Corozal, *J. M. & M. T. Greenman 5209* (MO); Camino de Corozal, *Bro. Heriberto 286* (US); vic of Miraflores Lake, *P. White 272* (F, MO); Balboa, *Standley 32109* (US); Sosa Hill, Balboa, *Standley 26414* (US). PANAMA: Las Sabanas, *Standley 25884* (US); Bella Vista, *Standley 25335* (US); vic of Bella Vista, *Piper 5339* (US); Tumba Muerto Road, nr Panama City, *Standley 29759* (US); vic of Juan Franco Race Track, nr Panama City, *Standley 27695* (US); along the Corozal Road, nr Panama City, *Standley 26795* (US); between Las Sabanas and Matías Hernández, *Standley 31882* (US); nr Matías Hernández, *Standley 28868* (US); nr the big swamp E of the Río Tocumen, *Standley 26699* (US); between Savannas and Río Yguana, *Macbride 2627* (F, US).

2. WISSADULA AMPLISSIMA (L.) R. E. Fries, K. Sv. Vetenskapsakad. Handl. [ser. 4] **43**(4): 48. 1908.

Sida amplissima L., Sp. Pl. 685. 1753.

Herb, suffrutex or shrub, the stem erect, to 1.5 m high, the branchlets very minutely tomentellous, the hairs whitish, simple (and glandular?) or stellate, and with scattered, long, stipitate, stellate hairs. *Leaves* short- (upper ones) to long-petiolate (lower ones), the petiole up to 8 cm long, covered with the same indumentum as the branchlets, the stipules subulate-filiform, up to 10 mm long, at length caducous; blade ovate to broadly ovate, deeply cordate and with the basal lobes often overlapping at the base, long-acuminate at the apex, the acumen blunt or acute, entire-margined, up to 12 cm long and 8 cm broad, gradually smaller toward the apex, membranous-chartaceous, strongly discolorous, velvety on both sides, 7- to 9-palminerved, the upper surface pale green (when dry) and minutely stellate-tomentellous, becoming glabrescent, the lower surface paler, densely whitish-stellate-tomentellous and with the venation reticulate and prominulous.

Flowers usually in lax, terminal, mostly leafless, paniculiform inflorescences, the pedicels slender, articulated above the middle, 0.5-2.5 cm long, to 3.5 cm long in fruit, densely and minutely glandular-puberulus; calyx campanulate, 3-4 mm long, minutely tomentellous with simple and stellate hairs, the lobes deltoid, acute, ca 1-1.5 cm long and broad at the base; petals obovate, ca 5 mm long and 2.5 mm broad, yellow, the claw minutely ciliolate; androecium ca 4 mm long, the staminal tube ca 2 mm long, minutely hyaline-hirtellous. *Fruit* turbinate, 5-lobed, constricted below the middle, the mericarps (3-4)5, 5.5-7.5 mm long, rigid-chartaceous, minutely puberulus, apiculate, the apiculum to 1 mm long; seeds angulate-subglobose, ca 2 mm in diam, minutely whitish-puberulus but whitish-pilose around the hilum.

West Indies and southern Texas to Brazil.

PANAMA: Taboga Island, moist thicket, *Standley 27038* (US).

3. WISSADULA EXCELSIOR (Cav.) Presl, Rel Haenk. **2:** 118, *t.69*(*a-m*). 1835.

Sida excelsior Cav., Mon. Cl. Diss. Dec. 27, *t.* 5 (3). 1785.

Herb or shrub, the stem erect, 0.6-2.4 m high, sparingly branched above, covered with 2 tiers of hairs, the lower tier of dense, minute, whitish or canescent, stellate hairs, the upper one of longer, stipitate, ferruginous, stellate hairs, the indumentum very dense when young. *Leaves* with the petiole much shorter than the blade, 0.25-8.5 cm long, covered with the same indumentum as the young branchlets, the stipules linear-subulate, 3-6 mm long; blade ovate or oblong-ovate, sometimes narrowly so, rounded or truncate or shallowly cordate with a very open sinus at the base, long-acuminate at the apex, the acumen acute or mostly blunt, entire-margined, 5-15 cm long and 2-8.5 cm broad, gradually smaller toward the apex, chartaceous, strongly discolorous, commonly 5-palminerved, the venation reticulate, the upper surface green or dark green, scabridulous, sparsely appressed-puberulus with simple and stellate hairs, at length glabrescent, and with the venation impressed, the lower surface pale, with 2 tiers of hairs, the lower tier minutely stellate-tomentellous with whitish or canescent hairs, the upper one ferruginous-stellate-pubescent with longer, stipitate hairs, the ferruginous hairs especially dense along the veins, and with the venation prominent. *Inflorescences* paniculiform, usually ∞-flowered, elongate, the axes and pedicels covered with the same indumentum as the young branchlets. *Flowers* rather short-pedicellate, the pedicel 0.5-1 cm long or shorter, slightly longer in fruit; calyx campanulate, lobed to about the middle, ca 3-4 mm long, covered with 2 tiers of hairs, minutely whitish-stellate-tomentellous and ferruginous-stellate-pubescent, the lobes deltoid, acute, ca 1.5-2 mm long and 1.2-1.5 mm broad at the base; petals obovate, 4-5 mm long and 2-3 mm broad, pale yellow, the claw minutely ciliolate; androecium ca 3-4 mm long, the staminal tube ca 1.5 mm long; styles ca 3.5-4 mm long, connate basally or almost free. *Fruit* turbinate, 5-lobed, constricted below the middle, the mericarps 5(6), 7-8 mm long, rigid-chartaceous, blackish at maturity, minutely puberulus, apiculate, the apiculum 0.5-0.8 mm long; seeds reniform-subglobose, 1.8-2 mm long, minutely puberulus but whitish-pilose around the hilum.

Cuba and southern Mexico to Peru and Brazil; trails and clearings, roadsides, moist thickets, brushy fields and slopes.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 510* (F, MO). CANAL ZONE: Obispo, *Standley 31782* (US); Empire to Mandinga, *Piper 5490* (US); vic of Summit, *Standley 30138* (US); Las Cascadas Plantation, nr Summit, *Standley 29684* (US); around Culebra, alt 50-150 m, *Pittier 2229* (US); along the old Las Cruces Trail, between Fort Clayton and Corozal, *Hunter & Allen 459* (MO), *Standley 29177* (US); vic of Corozal, *Piper 5301* (US); Balboa, *Standley 29321* (US). COCLÉ: N of El Valle de Anton, alt 700-800 m, *Allen 4214* (MO). PANAMA: hills between Capira and Potrero, alt 80-130 m, *Dodge & Hunter 8643* (F, MO, US); Las Sabanas, *Bro. Celestine 111* (US); Tumba Muerto Road, nr Panama City, *Standley 29761* (US); nr Matías Hernández, *Standley 28939* (US); between Matías Hernández and Juan Díaz, *Standley 31950* (US); Juan Díaz, *Standley 30520* (US); Río Tapía, *Standley 28051* (US); Río Tocumen, *Standley 29436* (US).

15. PSEUDABUTILON R. E. Fries

PSEUDABUTILON R. E. Fries, K. Sv. Vetenskapsakad. Handl. [ser. 4] **43**(4): 96. 1908.

Herbs or shrubs, the indumentum of stellate and often also simple hairs. *Leaves* petiolate (at least the lower ones), the stipules caducous, the blade cordate, the margins usually dentate, sometimes inconspicuously so. *Flowers* axillary and solitary, or in paniculiform, or spiciform inflorescences; epicalyx wanting; calyx 5-merous, campanulate or somewhat turbinate, lobed to about the middle, persistent; corolla small or medium-sized, the petals 5, the base adnate to the staminal tube; staminal tube short, ventricose, filamentiferous at the apex, the filaments numerous, the anthers reniform; ovary of 5-11 carpels, each carpel 3-ovulate, the ovules anatropous, pendulous; styles isomerous with the carpels, the stigmas capitate. *Fruits* stellate-turbinate or shortly cylindric, of 5-11 mericarps, these usually apiculate to rostrate apically, more or less divided into 2 superposed cavities by a transversal, membranous, tongue-like projection of the dorsal wall (endoglossum), the lower cavity with 1 seed, the upper with 2 collateral or superposed seeds, ultimately incompletely 2-valvate; seeds subglobose-reniform, glabrous or pubescent; embryo curved, the albumen scant.

An entirely American genus of about 15 species, ranging from southern Texas and the West Indies to Argentina. Only one species is at the present time reported from Panama.

1. PSEUDABUTILON SPICATUM (H. B. K.) R. E. Fries, K. Sv. Vetenskapsakad. Handl. [ser. 4] **43**(4): 98, *t.* 7(*19*). 1908.—Fig. 10.

Abutilon spicatum H. B. K., Nov. Gen. Sp. Pl. **5**: 271. 1822.
Wissadula spicata (H. B. K.) Presl, Rel. Haenk. **2**: 117. 1835.

Herb or suffrutex, annual or perennial, the stem erect, up to 2 m high, simple or sparingly branched, with 2 tiers of hairs, the lower tier stellate-tomentellous, the upper one hirsute with long, simple hairs, at length glabrescent. *Leaves* long-petiolate, the petiole terete, 3-15 cm long, covered with the same indumentum as the younger parts of stem and branches, the stipules linear-subulate, 6-10 mm

long, at length deciduous; blade circular or nearly so, infrequently sub-3-lobate, deeply cordate and with the basal lobes sometimes overlapping at the base, abruptly and rather long-acuminate at the apex, serrulate to subrepandous at the margin, 6-18 cm long and 5-16 cm broad, gradually smaller toward the apex, thin-chartaceous, slightly discolor, 7- to 9-palminerved, the upper surface green, stellate-puberulus and with the veins scarcely prominulous, the lower surface pale, softly canescent-stellate-subtomentellous and with the venation reticulate and prominulous. *Flowers* in very elongate, leafless, terminal panicles up to 40 cm long, with the secondary axes very short, thus simulating a spiciform inflorescence, the individual flowers subsessile to short-pedicellate, the pedicel to 2.5 mm long, in fruit to 4 mm long, articulated; calyx campanulate, ca 3 mm long, canescent-stellate-tomentellous, the lobes deltoid, acute, ca 1.5 mm long; petals obovate-cuneate, retuse at the apex, ca 6-7 mm long and 3-4 mm broad, yellow, the claw shortly ciliolate; androecium ca 4 mm long, the staminal tube ca 1.5 mm long, minutely

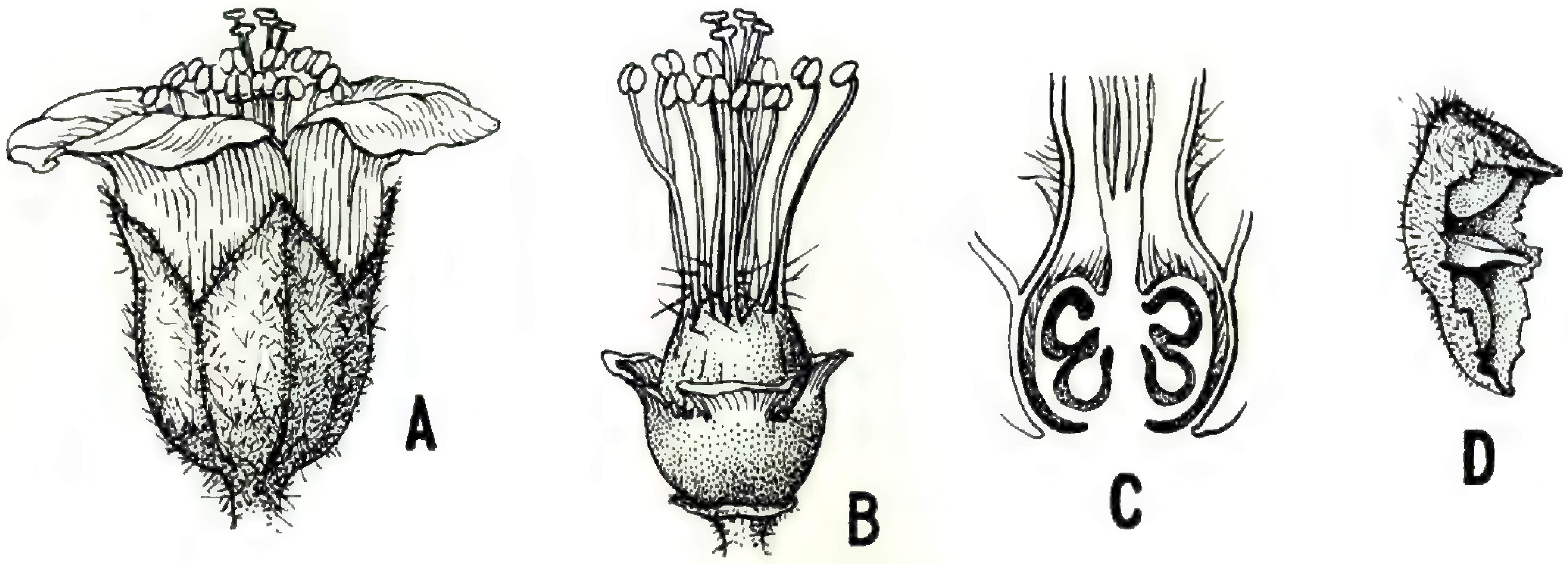

Fig. 10. PSEUDABUTILON SPICATUM (H.B.K.) R. E. Fries: A, flower (× 7½); B, id., calyx and corolla removed (× 7½); C, base of staminal tube and ovary, longitudinal section (ca × 12); mericarp (× 4½). After *Klug 4245* (MO) (Peru).

hyaline-puberulus; styles ca 3-4 mm long, basally connate. *Fruit* turbinate, the mericarps 5, trigonous, obpyramidal, more or less truncate and dorsally acute at the apex, ca 5 mm long, chartaceous, minutely stellate-puberulus; seeds collateral in the upper cavity, solitary in the lower one, ca 2 mm long, glabrous.

Cuba and Mexico to Brazil and Bolivia.

CANAL ZONE (or PANAMA?): along Chagres River, between Gamboa and El Vigía, alt 10-30 m, clearings, *Pittier 2365* (US). PANAMA: San José Island, on thin soil in an opening in a bit of deciduous forest, *Johnston 1141* (GH).

16. NEOBRITTONIA Hochr.

NEOBRITTONIA Hochr., Ann. Conserv. Jard. Bot. Genève **9:** 184. 1905.

Herbs or shrubs, the indumentum of stellate and simple hairs. *Leaves* long-petiolate, the stipules deciduous, the blade 3- to sub-5-palmatilobate, deeply cordate, the margins coarsely crenate-serrate. *Flowers* axillary, solitary, long-pedicel-

late; epicalyx wanting; calyx 5-merous, campanulate, lobed to below the middle, persistent and reflexed in fruit; petals 5, adnate to the base of the staminal tube; staminal tube ventricose, filamentiferous at the apex, the filaments numerous, the anthers hippocrepiform; ovary 9- to 12-carpellate, each carpel 2- or 3-ovulate; styles isomerous with the carpels, the stigmas capitate. *Fruits* subglobose to transversely ellipsoid, of 9-12 1-celled mericarps, these rounded and muticous at the apex, with 2 stout, basal and dorsal, deflexed awns, ultimately separating from the central axis but remaining attached thereto by subapical ligaments, bivalvate, 2- or 3-seeded; seeds cordiform-subglobose, muricate.

A monotypic genus which ranges from southern Mexico to Panama.

1. Neobrittonia acerifolia (G. Don) Hochr., Ann. Conserv. Jard. Bot. Genève **9:** 184, *pl. 1.* 1905.—Fig. 11.

Sida acerifolia Lagasca, Gen. Sp. Pl. 21. 1816, nomen illegitimum, non (Cav.) Medic. (1787).
Abutilon acerifolium G. Don, Gen. Syst. Gard. Bot. **1:** 504. 1831.
Sida discissa Bertol., Mem. Mat. Fis. Soc. Ital. Sci. (Modena) **23:** 305, *t. 5.* 1844.
Abutilon discissum (Bertol.) Schlecht., Linnaea **25:** 218. 1852.

Herb, woody below, or shrub, the stem erect, 1.5-3 m high, branched above, long-hirsute-hispid with mostly simple hairs, sometimes also with scattered, smaller, stellate hairs. *Leaves* with the petiole slender, terete, 1.5-20 cm long, gradually shorter toward the apex, long-hirsute-hispid and sometimes sparsely stellate-puberulus, the stipules subulate-filiform, ca 3 mm long; blade up to 22 cm long and 18 cm broad, gradually smaller toward the apex, the lobes obtuse or acute to long-acuminate, thin-chartaceous, nearly concolorous, 5- to 9-palminerved, strigose on both surfaces, the upper surface mostly with simple hairs, the lower surface densely stellate-puberulus and with the venation prominulous, the indumentum very dense when young. *Flowers* with the pedicel very slender, 2-9 cm long, long-hirsute and often also shortly stellate-puberulus; calyx ca 13-14 mm long, densely deflexed-hispid at the base, stellate-pubescent elsewhere, the lobes broadly ovate, acuminate, ca 8-9 mm long and 7 mm broad at the base; petals subcircular or transversely broadly elliptic, markedly unguiculate, the claw ca 4-5 mm long and densely barbate at the margins, the blade ca 11-13 mm long and 17-19 mm broad, lilac to purple; androecium ca 10 mm long, the staminal tube ca 5-6 mm long, densely villous. *Fruit* up to 2.5 cm high and 3 cm in diam at maturity, the mericarps greatly inflated, the basal awns up to 6 mm long, the pericarp thin-chartaceous and hispid with short and long, stellate hairs; seeds ca 3-3.5 mm long.

At high elevations only.

chiriquí: trail from Paso Ancho to Monte Lirio, upper valley of Río Chiriquí Viejo, alt 1500-2000 m, *Allen 1493* (MO); valley of the upper Río Chiriquí Viejo, *P. White 346* (MO).

17. ABUTILON Mill.

Abutilon Mill., Gard. Dict. Abridg. ed. 4. 1754.

Bogenhardia Reichenb., Repert. Herb. Nom. Gen. Pl. **1:** 200, **2:** 48. 1841; Kearney, Leafl. West. Bot. **7:** 119. 1954.
Gayoides (A. Gray) Small, Fl. Southeast. U. S. 764. 1903.
Pseudobastardia Hassl., Bull. Soc. Bot. Genève, sér. 2, **1:** 209. 1909.

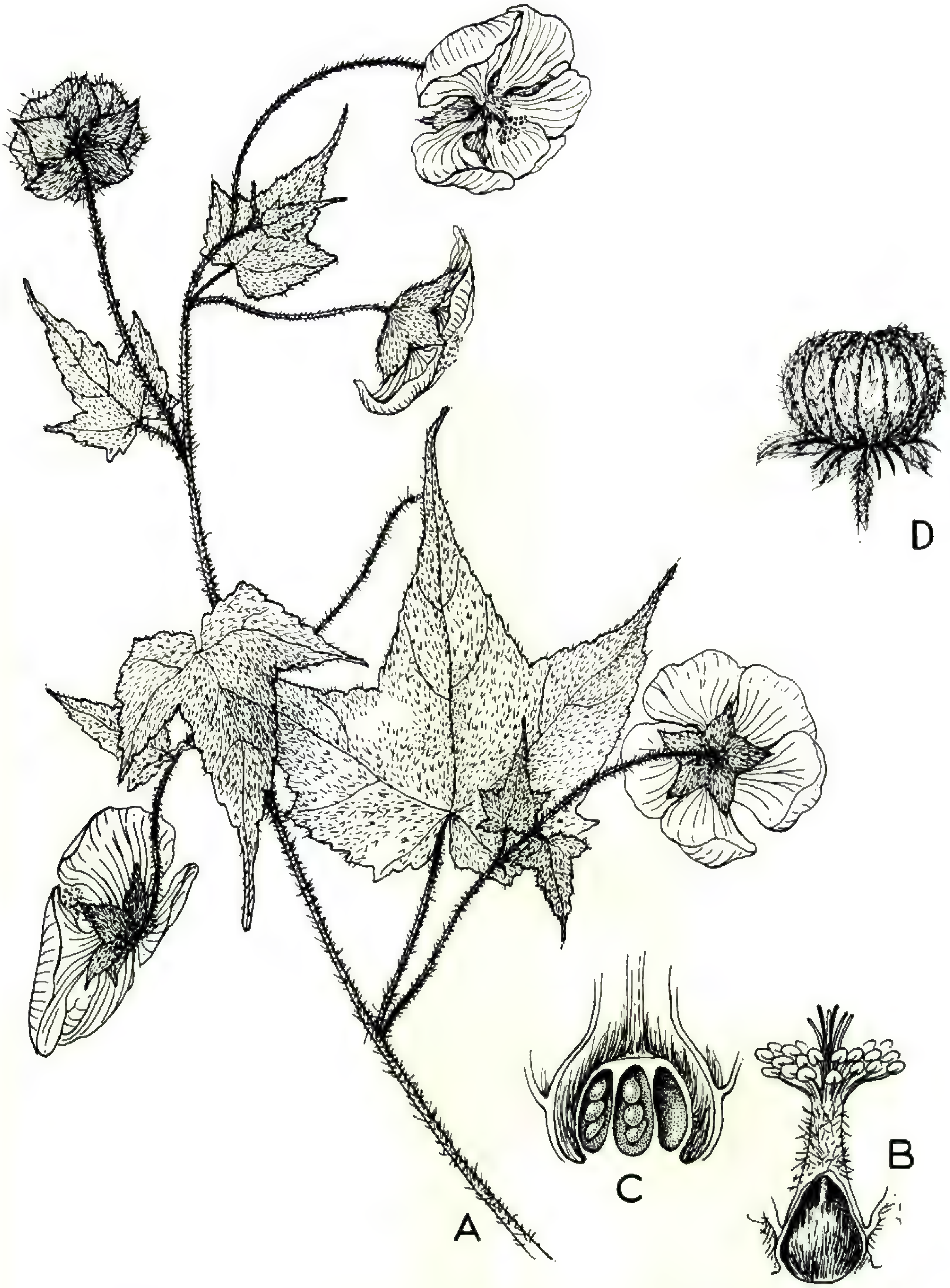

Fig. 11. NEOBRITTONIA ACERIFOLIA (G. Don) Hochr.: A, habit (× ¾), B, androecium and pistil (× 3); C, ovary, longitudinal section (× 6); D, fruit (× ¾). A-C after *Allen 1493*; D after *Pringle 8683* (MO) (Mexico).

Herbs, usually perennial, or shrubs or rarely small trees, the indumentum mostly of stellate hairs, these sometimes intermingled with longer, simple hairs. *Leaves* usually petiolate, the uppermost leaves sometimes sessile or nearly so, the stipules deciduous, the blade often cordate at the base. *Flowers* axillary and solitary, occasionally racemose on short, axillary branchlets, sometimes aggregated in terminal and axillary, leafy or leafless, paniculiform inflorescences; pedicels usually articulated, sometimes geniculate above the middle; epicalyx wanting; calyx 5-merous, campanulate to cupuliform, lobed usually to far below the middle, the lobes erect, patent or reflexed at anthesis, persistent or slightly accrescent; petals 5, adnate to the base of the staminal tube, patent or sometimes reflexed at anthesis; staminal tube often ventricose below, filamentiferous at and also often near the apex, the filaments numerous, the anthers reniform; ovary of 5-∞ carpels, each carpel with 2-several ovules, the ovules anatropous; styles isomerous with the carpels, the stigmas truncate to capitellate to capitate. *Fruits* subglobose to disciform, truncate or umbilicate at the apex, of 5-∞ 1-celled mericarps radially disposed around a central columella, the mericarps compressed laterally, inflated or not, muticous basally, muticous to aristate apically, separating ultimately from the central columella (but often remaining attached to the central columella long after maturity) and at length usually 2-valved, 3- to several-seeded; seeds superposed, more or less reniform, often asymmetrically so, the testa smooth to finely foveolate, glabrous or variously pubescent; embryo curved, the endosperm scant; cotyledons plicate.

A very large, pantropical genus, also widely distributed in subtropical regions. The species are so numerous in Mexico and Central America (cf. Kearney, A tentative key to the North American species of *Abutilon* Miller. Leafl. West. Bot. **7**: 241-254. 1955) and in northern South America, that it is rather surprising to find only six species, at present, reported from Panama, one of which is introduced from India.

a. Petals 6-13 mm long; mericarps 3-seeded.
  b. Calyx lobes and petals erect or patent at anthesis.
    c. Stems usually prostrate or ascending, infrequently erect; petals ca 6-7 mm long, white; staminal tube glabrous; mericarps greatly inflated, thin-chartaceous, rounded and muticous at the apex ....1. A. CRISPUM
    cc. Stems erect; petals ca 8-13 mm long, yellow or orange; mericarps not inflated, rigid-chartaceous, acute to long-aristate apically.
      d. Annual herbs; petals yellow or orange; staminal tube glabrous; mericarps long-aristate, the awns ca 3-5 mm long; introduced ..2. A. THEOPHRASTI
      dd. Shrubs; petals yellow; staminal tube stellate-arachnoid; mericarps acute to aristate apically, the awns up to 2 mm long.
        e. Calyx ca 11 mm long, the lobes narrowly ovate, acuminate, ca 10 mm long and 3.5 mm broad; petals ca 11 mm long, with indumentum; staminal tube ca 7 mm long, the filaments ca 2 mm long; styles ca 7-7.5 mm long; mericarps 10-12, ca 15 mm long ....3. A. CHIRIQUINUM
        ee. Calyx ca 7 mm long, the lobes triangular, acute, ca 4 mm long and broad at the base; petals ca 8 mm long, glabrous; staminal tube ca 4-5 mm long, the filaments 3-4 mm long; styles ca 5.5 mm long; mericarps ca 7, 10-11 mm long ....4. A. CYMOSUM

bb. Calyx lobes and petals reflexed at anthesis; stems erect; petals ca 10 mm long, white; staminal tube glabrous; mericarps not inflated, rigid-chartaceous, acute apically .... 5. A. GIGANTEUM
aa. Petals ca 3 cm long, pale yellow; mericarps several-seeded .... 6. A. PURPUSII

1. ABUTILON CRISPUM (L.) Medic., Malv.-Fam. 29. 1787.

Sida crispa L., Sp. Pl. 685. 1753.
Gayoides crispum (L.) Small, Fl. Southeast. U. S. 764. 1903.
Pseudobastardia crispa (L.) Hassler, Bull. Soc. Mot. Genève, ser. 2, **1:** 211. 1909.
Bogenhardia crispa (L.) Kearney, Leafl. West. Bot. **7:** 120. 1954.

Herb or shrub, the stem slender, usually prostrate or ascending, infrequently erect, up to 1.2 m long, hirsute-velutinous, the hairs mostly simple, sometimes also sparsely stellate-puberulus. *Leaves* long-petiolate (lower leaves) to sessile and amplexicaul (upper leaves), the petiole up to 8 cm long and with the same indumentum as the stem, the stipules subulate-filiform, 2.5-3 mm long, at length deciduous; blade ovate, deeply cordate at the base, long-acuminate at the apex, irregularly crenulate to crenate or serrate, up to 11 cm long and 6.7 cm broad, gradually smaller toward the apex of the stem and branchlets, slightly discolor, 5- to 9-palminerved, both surfaces soft, the upper surface more or less densely stellate-puberulus and with the venation scarcely impressed, the lower surface slightly paler, more or less densely stellate-tomentellous and with the venation reticulate and prominent. *Flowers* axillary, solitary, the pedicels elongate, very slender, articulated and geniculate above the middle, up to 2 cm long, hirsute and stellate-puberulus, the indumentum denser above the articulation; calyx broadly campanulate, shallowly 5-angled basally, ca 5.5 mm long, stellate-tomentellous, the lobes ovate, acuminate, ca 3.5-4 mm long and 2.5-2.7 mm broad at the base, persistent and reflexed in fruit; petals broadly obovate-cuneate, rounded to subacute at the apex, ca 6-7 mm long and 4-5.5 mm broad, white, the claw margins ciliolate; androecium ca 4-5 mm long, the staminal tube angulate-ovoid, ca 3 mm long, membranous, glabrous, the anthers reniform, very minutely brown-red papillate; styles ca 3.5-4.5 mm long, almost free or connate basally for ca 1.5-2 mm, the stigmas capitellate. *Fruit* depressed-globose, 10-18 mm in diam, the mericarps ca 10, reniform, rounded and muticous above and below, greatly inflated, 8-12 mm long, the pericarp thin-chartaceous and setose with mostly simple hairs, ultimately separating from the central, persistent columella and bivalvate, the valves of adjacent pairs remaining connate, 3-seeded; seeds cordiform-subglobose, ca 1.5-1.8 mm long, finely alveolate and minutely puberulus, the hairs bulbous at the base.

Southern United States to Bolivia and Argentina; brushy slopes, clearings, and roadsides, usually in dry soil.

CANAL ZONE: Ancon Hill, *Standley 25188* (US). HERRERA: vic of Ocú, alt 100 m, *Allen 4091* (F, MO). PANAMA: nr beach at Nueva Gorgona, *Duke 4494* (MO); Taboga Island, *Macbride 2768* (F, US), *Standley 27957* (US); Taboguilla Island, *Miller 1991* (MO, US); San José Island, *Johnston* 673 (US).

2. ABUTILON THEOPHRASTI Medic., Malv.-Fam. 28. 1787; Johnston, Sargentia **8:** 195. 1949.

Sida abutilon L., Sp. Pl. 685. 1753.
Abutilon avicennae Gaertn., Fruct. Sem. **2:** 251, *t. 135.* 1791.

Herb, annual, the stem erect, 0.3-1.2 m high, more or less tomentose, the hairs simple and/or stellate. *Leaves* long-petiolate, the petiole rather slender, usually longer than the blade, more or less tomentose, the stipules early caducous; blade broadly ovate to subcircular to very broadly ovate, deeply cordate at the base, more or less abruptly long-acuminate at the apex, crenulate or crenate-dentate at the margin, up to 20 cm broad, chartaceous, slightly discolor, 7- to 9-palminerved, puberulus and usually with stellate hairs on both surfaces but the indumentum usually softer and denser beneath, the veins prominent beneath. *Flowers* axillary and solitary, or in a few-flowered, leafy, terminal panicle, the pedicels shorter than the petioles, articulate usually above the middle, tomentose; calyx broadly campanulate, ca 10 mm long, tomentose, lobed to far beyond the middle, the lobes patent at anthesis, ovate and acute, accrescent; petals patent at anthesis, oblong-obovate, ca 10-13 mm long, yellow or orange, glabrous at the insertion of the staminal tube; androecium shorter than the calyx and corolla, the staminal tube much inflated, glabrous. *Fruit* broadly cylindric, umbilicate, villous to densely pubescent, the mericarps about 15, 12-15 mm long (awns excluded), long-aristate at the apex, the awns widely spreading and ca 3-5 mm long, rounded at the base, rigid-chartaceous, 3-seeded; seeds ca 3.5-4 mm long, inconspicuously foveolate and minutely puberulus.

A weed native to India, but introduced and fully naturalized in many regions in North America; apparently of recent introduction on San José Island.

PANAMA: San José Island, *Johnston 1353* (GH).

3. ABUTILON **CHIRIQUINUM** A. Robyns, sp. nov.

Frutex erectus, 1-3 m altus, plus minusve dense hirsutus pilis simplicibus et saepe plus minusve retrorsis, plerumque etiam sparse stellato-puberulus. *Folia* longe petiolata petioloque tereti usque ad 9.5 cm longo caulis et ramulorum apicem versus sensim breviore tenuioreque sed nunquam folia sessilia dense hirsuto plerumque etiam sparse stellato-puberulo, stipulis mox deciduis; lamina late ovata ovatave, basi plerumque profunde cordata interdumve subcordata, apice longe acuminata, marginibus irregulariter subcrenatis ad denticulatis, usque ad 13.5 cm longa et 11 cm lata, caulis ramulorumque apicem versus sensim minor, tenuiter chartacea, leviter discolor, 7-9-palminervis, supra plus minusve dense pubescens pilis praecipue simplicibus adpressis patentibusve, infra pallidiora et molliter stellato-tomentosa ad stellato-pubescens nervisque reticulatis prominentibus pilis simplicibus patentibus instructis. *Flores* primum axillares solitariique, dein in ramulis accessoriis racemosi paniculiformesque inflorescentias formantes; gemmae ovoideae longeque acuminatae; pedicellus gracilis, usque ad 1.5 cm longus, in fructu longior, supra medium articulatus, hirsutus et minute stellato-puberulus; calyx late campanulatus, ca 11 mm longus, dense minuteque stellato-puberulus et hirsutus, ultra medium in lobos anguste ovatos acuminatos ca 10 mm longos basi 3.5 mm latos in fructu refractos divisus; petala patentia, obovato-cuneata, ca 11 mm longa et 7-7.5 mm lata, flava, praecipue apicem versus sparse stellato-puberula, ad insertionem tubi staminei villosa; tubus stamineus basi valde inflatus, ca 7 mm

longus, minute stellato-arachnoideus, filamentis ca 2 mm longis; styli ca 7-7.5 mm longi, infra medium connati. *Fructus* late stellato-cylindricus, umbilicatus, ca 15 mm longus et 12 mm diam, mericarpiis 10-12 apice dorsaliter acutis ad aristatis aristisque usque ad 2 mm longis basi rotundatis rigide chartaceis hirsutis 3-spermis; semina ca 2 mm longa inconspicue foveolata et sparse minuteque puberula.

Native to the Province of Chiriquí, growing among bushes and on waste land at altitudes of about 990-1350 m.

CHIRIQUÍ: Alto Lino, vic of El Boquete, alt 990 m, *Bro. Maurice 705* (holotype US, isotype MO); Bajo Mono, elev 4500 ft, *M. E. Davidson 477* (F, MO, US); around El Boquete, alt 100-1300 m, *Maxon 4928* (US), *Pittier 2885* (US).

This new species is closely related to *A. giganteum* (Jacq.) Sweet and *A. cymosum* Triana & Planchon. It is readily distinguished from the former by its patent calyx lobes and petals at anthesis, the yellow corolla, the minutely stellate-arachnoid staminal tube, and its habitat. From the latter it differs chiefly in having larger flowers—especially longer and narrower calyx lobes—and fruits, and in the indumentum.

4. ABUTILON CYMOSUM Triana & Planchon, Ann. Sci. Nat., Bot., sér. 4, **17:** 185. 1862.

A. rufinerve sensu Seem., Bot. Voy. Herald 83. 1854, non St.-Hil. *et al.* (1827).

Shrub 1.2-1.8 m high, the stem erect, arachnoid-pubescent with chiefly stellate hairs. *Leaves* with the petiole terete, up to 3 cm long, pubescent with mostly stellate hairs, the stipules subulate, ca 3 mm long, early caducous; blade ovate, cordate at the base, gradually long-acuminate at the apex, serrate at the margin, up to 9 cm long and 4.5 cm broad, gradually smaller toward the apex of the stem and branchlets, chartaceous, slightly discolorous, the upper surface slightly scabridulous-puberulus, the lower surface paler and softly arachnoid-pubescent, the hairs simple and stellate, 5- to 7-palminerved, the venation slightly impressed above (at least when young) and prominulous beneath. *Flowers* at first axillary and solitary, later accompanied by a racemose flowering branchlet, forming altogether an ample, terminal, paniculiform inflorescence; pedicel 5-8 mm long, up to 12 mm long in fruit, articulated above the middle, finely stellate-puberulus and also viscid-pubescent with simple hairs; calyx campanulate, ca 7 mm long, densely and finely stellate-puberulus and often also sparingly viscid-pubescent with simple hairs, lobed to slightly below the middle, the lobes triangular, acute, ca 4 mm long and broad at the base; petals erect, obovate-cuneate, rounded at the apex, ca 8 mm long and 5-6 mm broad, yellow, glabrous; staminal tube ventricose below, ca 4-5 mm long, rigid-stellate-arachnoid, the filaments ca 3-4 mm long; styles ca 5.5 mm long, connate for ca 3.5 mm. *Fruit* stellate-cylindric, umbilicate, 10-11 mm long and 7-8 mm in diam, the mericarps ca 7, rounded at the base, awned at the apex, the awns up to 2 mm long, rigid-chartaceous, rigid-stellate-pubescent and also with simple, viscid hairs; seeds ca 1.7-1.8 mm long, inconspicuously foveolate, glabrous.

Panama and Colombia.

CHIRIQUÍ: Boquete, *Seemann 1628* (lectotype K).

The label on the Seemann's collection reads as follows: "*1628*. Boquete, Veraguas, febr. 1849," while the citation in Seemann's Flora of the Isthmus of Panama (Bot. Voy. Herald 83. 1854) is: "Volcano of Chiriquí, Veraguas."

5. Abutilon giganteum (Jacq.) Sweet, Hort. Brit. **1:** 53. 1826.

Sida gigantea Jacq., Pl. Rar. Hort. Caes. Schoenbr. Descr. Ic. **2:** 8, *t. 141.* 1797.

Herb, shrub or small tree, up to 6 m high, the branchlets yellowish-stellate-tomentose. *Leaves* with the petiole rounded, 2-4 cm long, stellate-tomentose, the stipules early caducous; blade ovate, sometimes slightly asymmetric, deeply cordate at the base, gradually long-acuminate at the apex, crenulate-denticulate at the margin, 5-12.5 cm long and 2.5-7.5 cm broad, gradually smaller toward the apex of the stem and branchlets, chartaceous, concolorous or nearly so, usually 9-palmi-nerved, the upper surface more or less densely stellate-pubescent, becoming glabrescent, the lower surface softly stellate-arachnoid and with the venation slightly prominent. *Flowers* at first axillary and solitary, later accompanied by a racemose flowering branchlet, forming altogether an ample, leafless, terminal, paniculiform inflorescence, the axes yellowish-stellate-tomentose; pedicel stout, articulate, up to 1.5 cm long but usually shorter along the racemose flowering branchlets, densely yellowish-stellate-tomentose; calyx broadly campanulate, ca 12 mm long, yellowish-stellate-velutinous, deeply lobed, the lobes reflexed at anthesis, ovate, acute, ca 10 mm long and 5 mm broad, accrescent; petals reflexed at anthesis, obovate, equalling more or less the calyx, white, villous at the insertion of the staminal tube and forming a ring of hairs around the tube; androecium ca 12 mm long, the staminal tube enlarged below, ca 8 mm long, glabrous, the filaments ca 4 mm long; styles ca 9 mm long, connate below the middle. *Fruit* broadly cylindric, umbillicate, ca 1 cm long and in diam, stellate-tomentellous to densely stellate-puberulus, the mericarps 8-14, acute at the apex, rounded at the base, rigid-chartaceous, 3-seeded; seeds ca 2-2.5 mm long, hispidulous.

West Indies and southern Mexico to northern South America.

PANAMA: Cerro Campana, *Allen 2094* (F, MO, US).

6. Abutilon purpusii Standl., Contr. U. S. Nat. Herb. **23:** 750. 1923.

A. jaliscanum Standl., Field Mus. Nat. Hist., Bot. Ser. **4:** 229. 1929.
A. brenesii Standl., loc. cit. **18:** 664. 1937.

Shrub or small tree, 2-5 m tall, the branchlets slender, terete, green, stellate-tomentellous to densely stellate-puberulus, the internodes elongate. *Leaves* long- (lower ones) to short-petiolate (upper ones), the petiole terete, 1-12 cm long, stellate-tomentellous to densely stellate-puberulus, the stipules early caducous; blade broadly ovate to ovate, deeply cordate and with an open sinus at the base, long-acuminate at the apex, coarsely crenate to serrate or serrulate or denticulate at the margin, sometimes only very shallowly so, up to 25 cm long and 19 cm broad, gradually smaller toward the apex of the branchlets, thin-chartaceous,

slightly discolor, 7- to 9-palminerved, the upper surface scabridulous and sparsely puberulus to glabrescent, the lower surface slightly paler, softly stellate-tomentose to densely stellate-pubescent, and with the venation reticulate and prominent. *Flowers* solitary (infrequently geminate) in the upper leaf axils, long-pedicellate, the pedicel terete, articulated near the apex and often more or less nodding above the articulation, 2-6 cm long, stellate-tomentellous, the indumentum especially dense above the articulation, the fruiting pedicel somewhat longer and thicker; calyx broadly campanulate, ca 18-20 mm long, brownish- or fulvous-stellate-tomentellous, lobed to far beyond the middle, the lobes patent at anthesis, ovate, acuminate, ca 15 mm long and 8 mm broad; petals patent at anthesis, obovate-unguiculate, ca 3 cm long and 2 cm broad, pale yellow, the claw glabrous or almost so; androecium equalling more or less the corolla, the staminal tube glabrous, filamentiferous at and near the apex, the filaments very numerous and ca 4-5 mm long; styles ca 3 cm long, connate below the middle. *Fruit* of 7-many mericarps, these rounded to subacute at the apex, 2-3 cm high, rigid-chartaceous, stellate-tomentellous to densely stellate-puberulus, several-seeded; seeds ca 2.5-3 mm long, hispidulous, the hairs simple or few-forked.

Southern Mexico, Guatemala, Costa Rica and Panama; called *algodoncillo* in Panama (fide *Bro. Maurice 721*).

CHIRIQUÍ: Alto Lirio, vic of El Boquete, alt 990 m, *Bro. Maurice 721* (US); Bajo Mono, elev 4500 ft, *M. E. Davidson 498* (F, US).

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 118. DILLENIACEAE[1]

BY GORDON E. HUNTER

Murray State College, Murray, Kentucky

Lianas, shrubs or trees, often copiously pubescent or scabrous. *Leaves* alternate, petiolate, simple, frequently coriaceous, penninerved, estipulate. *Inflorescences* thyrsiform, paniculiform or obscurely glomerulate. *Flowers* hypogynous, perfect or unisexual, actinomorphic, the sepals 3-7, frequently 5, the petals 2-6, yellow, white or rarely pinkish, usually emarginate or incised, often somewhat crumpled in the bud, caducous (except in *Saurauia*), the stamens indefinite, free or fused at the base (adnate to the corolla in *Saurauia*), the anthers basifixed and longitudinally dehiscent, or bifurcate, versatile and basally dehiscent by rimiform pores, the carpels 1-5, free to fused, the ovules 1 to several, anatropous, basal, and erect (numerous and axile in *Saurauia*), the styles free, as many as the carpels, the stigmas apical, simple to capitate or peltate. *Fruits* follicular to baccate, the seeds 1-∞, arillate (nonarillate in *Saurauia*), embedded in copious mealy or fleshy endosperm.

a. Lianas or scandent shrubs (except the often arborescent *Curatella*); petals free, caducous; stamens free to basally fused, the anthers longitudinally dehiscent, the thecae completely adnate to the thickened connective; carpels 1-5, free or basally fused; fruits usually dehiscent, the seeds large, few, smooth, arillate; trichomes simple and stellate, multicellular hairs lacking.
  b. Leaves scabrous; flowers unisexual; carpels pyriform, 1-5, the ovules several per carpel; follicles dehiscing ventrally; seeds 1-few, the aril lacerate, unilateral and about half enveloping the seed .... 1. TETRACERA
  bb. Leaves scabrous or smooth; flowers perfect; carpels globose, 1-2, the ovules 2; seeds 1-2, the aril essentially entire, nearly enveloping the seed.
    c. Sepals unequal, the inner 2 accrescent and enclosing the usually persistent stamens in fruit; fruit irregularly dehiscent, 1-seeded .... 2. DAVILLA
    cc. Sepals nearly equal, not enclosing the usually persistent stamens in fruit; fruit dehiscing longitudinally across the apex, the carpels each with 2, rarely 1 seed.
      d. Small trees or shrubs; leaves stellate-pubescent on both sides, scabrous; inflorescence diffusely paniculiform; carpels 2 .... 3. CURATELLA
      dd. Lianas and scandent shrubs; leaves glabrous or pubescent with simple hairs, smooth; inflorescence obscurely glomerulate; carpels 1 .... 4. DOLIOCARPUS

aa. Trees and shrubs; petals connate at the base, falling as a unit with the stamens; anthers versatile, dehiscent by rimiform pores, the locules free from the connective except at the apex; carpels fused, the styles free; fruit baccate, the seeds small, many, areolate, nonarillate; trichomes multicellular, stellate and simple .... 5. SAURAUIA

[1]Assisted by NSF Grants No. G-7144 (Principal Investigator R. E. Woodson, Jr.) & No. GB-170 (Principal Investigator H. C. Cutler)

1. TETRACERA L.

Tetracera L., Sp. Pl. 533. 1753.

Tragia Stickman in L., Herb. Amboinense 18. 1754, non L. (1753).
Delima L., Gen. Pl. ed. 5, 231. 1754.
Korosvel Adans., Fam. Pl. **2:** 442. 1763.
Assa Houtt., Nat. Hist. **2**(5): 275, *t. 26(1)*. 1775.
Euryandra Foster & Foster, Char. Gen. Pl. 81, *t. 41*. 1776.
Actaea Lour., Fl. Cochinch. 332. 1790, non L. (1753).
Seguieria Lour., loc. cit. 341, non Loefl. (1758).
Calligonum Lour., loc. cit. 342, non L. (1753).
Wahlbomia Thumb., K. Sv. Vet.-akad. Handl., ser. 2, **11:** 215, *t. 9*. 1790.
Trachytella DC., Reg. Veg. Syst. Nat. **1:** 410. 1817.
Traxilisa Rafin., Sylva Tellur. 161. 1838.
Diploter Rafin., loc. cit. 165.
Eleiastis Rafin., loc. cit.
Gynetera Rafin., loc. cit.
Leontoglossum Hance in Walp., Ann. Bot. Syst. **2:** 18. 1851.
Delimopsis Miq., Fl. Ind. Bat. **1**(2): 9. 1858.

Lianas or scandent shrubs. *Leaves* alternate, usually scabrous, pubescent with simple or stellate hairs more or less incrusted with silica, the petioles often canaliculate and narrowly alate. *Inflorescences* axillary or terminal, paniculiform, many-flowered. *Flowers* unisexual, actinomorphic, the pistillate with many apparently sterile hypogynous stamens; sepals usually 5, persistent, more or less equal or the outer slightly smaller; petals 2-5, caducous; stamens 50-200, multiseriate, persistent, the filaments free to basally fused, filiform, the anthers longitudinally dehiscent, the outermost frequently sterile, 2-thecate, the thecae nearly parallel to basally divergent, about half sunken into the dilated connective; carpels 1-5, pyriform, free, 1-loculed, the ovules 2-12, more or less erect on 2, seldom 3, ventral placentas, the styles filiform, exceeding the stamens in pistillate flowers, the stigmas capitate, frequently somewhat emarginate. *Follicles* 1-5, pyriform, dry, dehiscing along the ventral suture, the seeds 1-4, smooth, arillate, the aril lacerate, unilateral, about half enveloping the seed, the embryo small, straight.

Numerous species in the tropics of both hemispheres.

Tetracera is often misidentified as *Davilla* Vand. The lack of carpels in the male flowers and the pyriform carpels of the female, however, easily distinguish it from the latter with its perfect flowers and solitary globose carpels. In fruit, it is even easier to distinguish, because the sterile stamens of *Tetracera* are still visible beneath the carpels, while the stamens of *Davilla* are hidden by the two accrescent inner sepals which envelope them and the fruit.

a. Secondary veins of the leaves usually less than 15 pairs; petioles usually longer than 10 mm; flowers pedicellate; stamens 120-200; carpels 2-5.
  b. Leaf blades frequently subattenuate, the petioles distinctly alate to the axil; sepals densely pubescent within; carpels brown .... 1. T. VOLUBILIS
  bb. Leaf blades truncate to obtuse, the petioles alate on the upper half; sepals glabrous to slightly pubescent within; carpels tawny .... 2. T. OVALIFOLIA
aa. Secondary veins of the leaves 15-25 pairs; petioles usually shorter than 10 mm; flowers subsessile; stamens 50-80; carpels 1, brown; sepals glabrous to slightly pubescent within .... 3. T. PORTOBELLENSIS

1. TETRACERA VOLUBILIS L., Sp. Pl. 533. 1753.

T. jamaicensis DC., Reg. Veg. Syst. Nat. **1:** 399. 1817.
T. erecta DC., loc. cit. 404.
T. Poeppigiana Schlecht., Linnaea **8:** 174. 1833.
T. salicifolia Presl, Rel. Haenk. **2:** 71. 1835.
T. alata Presl, loc. cit.
T. mexicana Eichl. in Mart., Fl. Bras. **13**(1): 87. 1863.

Liana or rarely shrub. *Leaves* with the blade obovate, the apex acuminate to obtuse, the base acute to subattenuate, the margins entire to serrate, 9-20 cm long, 5-8 cm wide, chartaceous, pustulate, the pustules heavily incrusted with silica and bearing a simple or stellate hair at the center, the secondary veins 10-25; petioles 10-20 mm long, distinctly alate to the axil. *Flowers* 5-12 mm broad, pedicellate, rarely subsessile; sepals 5, elliptic to ovate, 2-5 mm long, 2-3 mm wide, densely pubescent with filiform hairs within; stamens 120-200, the filaments 5 mm long, the thecae ca 0.5 mm long, basally divergent; carpels 4-5, pyriform, the styles 2 mm long, the stigmas peltate, emarginate. *Follicles* glabrous to apically barbate, dark brown, 6-8 mm long, 3-4 mm wide, the persistent styles 1-2 mm long.

Southern Mexico and the Antilles to northern Brazil.

CANAL ZONE: Barro Colorado Island, *Aviles 9* (F), *Ebinger 27* (MO), *Killip 40005* (US), *Wetmore & Abbe 182* (F); nr El Vigia & San Juan on Río Pequeni, *Dodge et al. 16575* (MO); Balboa, *Standley 29261* (US); Chagres, *Fendler 27* (MO, US); old Las Cruces Trail, between Fort Clayton & Corozal, *Standley 29170* (US); K-9 road, at large bridge, *Dwyer 3010* (MO). COCLÉ: outside of Penonomé, *Ebinger 1002* (MO); Penonomé and vic, *R. S. Williams 94* (US). DARIEN: 1-3 mi SE of Santa Fe on Pan-Am. Highway, Río Sabana, *Duke 4120* (MO). PANAMA: Cerro Chame, *Allen 2242* (MO, US); Laguna de Portalo, nr Chepo, *Pittier 4745* (US); Las Sabanas, *Bro. Paul 93* (US), *Standley 25861* (US); Río Las Lajas, *Allen 2039* (MO, US); Sabana de Juan Corso, nr Chepo, *Pittier 4540* (US); San José Island, *Harlow 42* (US), *67* (US), *100* (US), *Johnston 391* (US), *522* (MO, US), *1075* (MO, US); Pan-Am. Highway just E of Bejuco, *Duke 4549a* (MO); Isla de Pedro Gonzales, *Dwyer 1678* (F); E of Río Tocumen, *Standley 26251* (US); vic of Juan Franco Race Track, nr Panama, *Standley 27707* (US); Punta Paitilla, *Piper 5415* (US), *Standley 30791* (US).

2. TETRACERA OVALIFOLIA DC., Reg. Veg. Syst. Nat. **1:** 400. 1817.

T. rotundifolia J. E. Sm. in Rees, Cyclopaedia **35.** 1817.
T. fagifolia Willd. ex Schlecht., Linnaea **8:** 174. 1833.
T. Willdenowiana Steud., Nom. Bot. ed. 2, **2:** 670. 1841.
T. surinamensis Miq., Linnaea **18:** 265. 1844.
T. hydrophila Triana & Planchon, Ann. Sci. Nat., Bot., sér. 4, **17:** 20. 1862.
T. belizensis Lundell, Contr. Univ. Mich. Herb. **6:** 44. 1941.

Liana. *Leaves* with the blade elliptic, the apex shortly acuminate to obtuse, the base obtuse to truncate, the margins entire, sometimes becoming serrulate toward the apex, 7-17 cm long, 4-9 cm wide, chartaceous, minutely pustulate, the secondary veins 9-14 pairs; petioles 15-35 mm long, alate on the upper half. *Flowers* 10-15 mm broad, pedicellate; sepals 5, obovate, 3-5 mm long and wide, glabrous to slightly pubescent within, minutely pustulate without; petals 4-5, white, elliptic to obovate, 7-9 mm long, 3-5 mm wide; stamens 150-200, the filaments 5 mm long, the thecae ca 0.5 mm long, basally divergent; carpels 2-5, pyriform, the styles 1-2 mm long, the stigmas simple. *Follicles* 2-5, glabrous, tawny, 6-8 mm long, 3-5 mm wide, the persistent styles 2-3 mm long.

BOCAS DEL TORO: Water Valley, vic of Chiriquí Lagoon, *von Wedel 1664* (F, MO), *1759* (MO), *2150* (MO); Cricamola Valley, region of Almirante, *Cooper 204* (F); Laguna de Chiriquí and vic, *Hart 134* (US). CANAL ZONE: Barro Colorado Island, *Shattuck 241* (F); vic of Hill C-6, Fort Sherman, *Duke 4383a* (MO). PANAMA: San José Island, *Johnston 309* (MO).

I. M. Johnston in his study of San José Island (Sargentia **8:** 205. 1949) chose the specific epithet *fagifolia* Willd. which is representative of this population but is a later homonym of an Asian species. Delessert's figure (Ic. Sel. Pl. **1:** *t.* 68. 1820) and de Candolle's description of *T. ovalifolia* are in close agreement with the characteristics of the Central American population.

3. Tetracera portobellensis Buerling, K. Sv. Vet.-akad. Handl. 1854: 113. 1854(?).—Fig. 1.

Delima mexicana DC., Reg. Veg. Syst. Nat. **1:** 407. 1817.
Tetracera volubilis H. B. K., Nov. Gen. Sp. Pl. **5:** 50. 1821, non L. (1753).
T. sessiliflora Triana & Planchon, Ann. Sci. Nat., Bot., sér. 4, **17:** 21. 1862.

Liana or shrub. *Leaves* with the blade elliptic to obovate, the apex shortly acuminate to obtuse, the base attenuate, the margins serrate to serrulate, 10-18 cm long, 4-8 cm wide, chartaceous, pustulate, the pustules heavily incrusted with silica and giving rise to many-rayed stellate hairs, the secondary veins 15-25; petioles 3-10 mm, rarely to 15 mm long, alate. *Flowers* 5 mm broad, subsessile; sepals 5, obovate, 2-3 mm long and wide, densely pubescent without, glabrous to slightly pubescent within; petals 2-4, white to greenish, narrowly obovate, 5 mm long, 2 mm wide; stamens 50-80, the filaments 4 mm long, the thecae 0.2-0.3 mm long, basally divergent; carpels 1, pyriform, the style 1-2 mm long, the stigma somewhat expanded and flattened. *Follicle* 1, glabrous, dark brown, 5-7 mm long, 3-4 mm wide, the persistent style 2-3 mm long.

Jalisco, Mexico to Bolivia and northern Brazil.

BOCAS DEL TORO: Bar Mouth, Changuinola Valley, *Dunlap 516* (F); Isla Colón, *von Wedel 76* (MO); Water Valley, vic of Chiriquí Lagoon, *von Wedel 1909* (MO, US). CANAL ZONE: Darien Station, *Standley 31526* (US), *31631* (US); Gatun Station, *Hayes s.n.* (US), *14* (MO, US), *16* (US); Gatun, *Ostenfeld 45* (US); hills W of the Canal, nr Gatun, *Standley 27280* (US); Upper Río Pequení between Salamanca Hydrographic Station & Río Boquerón, *Allen 17284* (MO); nr Old Fort Lorenzo, mouth of Río Chagres, *Piper 5907* (US); Barro Colorado Island, *Bailey & Bailey 264* (F), *Shattuck 747* (F, MO, US); nr Bohio, *Maxon 4768* (US). COLÓN: along Río Fato, *Pittier 3874* (US). DARIEN: around Garachiné, *Pittier 5506* (US).

In the Index Kewensis *Delima mexicana* DC. and *Tetracera sessiliflora* Triana & Planchon are given as synonyms. De Candolle's description and the icones of the Mociño and Sessé collections leave no doubt that *D. mexicana* is, indeed, conspecific with *T. sessiliflora,* and thus a synonym of *T. portobellensis.*

2. DAVILLA Vandelli

Davilla Vandelli, Fl. Lusit. Bras. 35. 1788.
Hieronia Vell., Fl. Flum. 234. 1825, Fl. Flum. Ic. **5:** *t. 116.* 1835.

Lianas to small trees. *Leaves* alternate, frequently scabrous, pubescent with simple hairs only, the petioles often canaliculate, narrowly alate. *Inflorescences*

axillary or terminal, paniculiform, usually many-flowered. *Flowers* perfect, actinomorphic; sepals 5, unequal, the inner 2 accrescent, enveloping the fruit and the persistent stamens at maturity; petals 1-6, caducous; stamens indefinite, persistent, the filaments free, filiform, the anthers longitudinally dehiscent, 2-thecate, the thecae nearly parallel, about half sunken into the dilated connective; carpels 1, globose, 1-loculed, the ovules 2, erect, basal, the styles clavate, exceeding the stamens, the stigmas peltate, emarginate. *Fruit* globose, indehiscent to irregularly dehiscent, the seeds 1, smooth, arillate, the aril more or less entire, completely enveloping the seed at maturity, the embryo small, straight.

Restricted to the American tropics and the Antilles with 2 species in Central America.

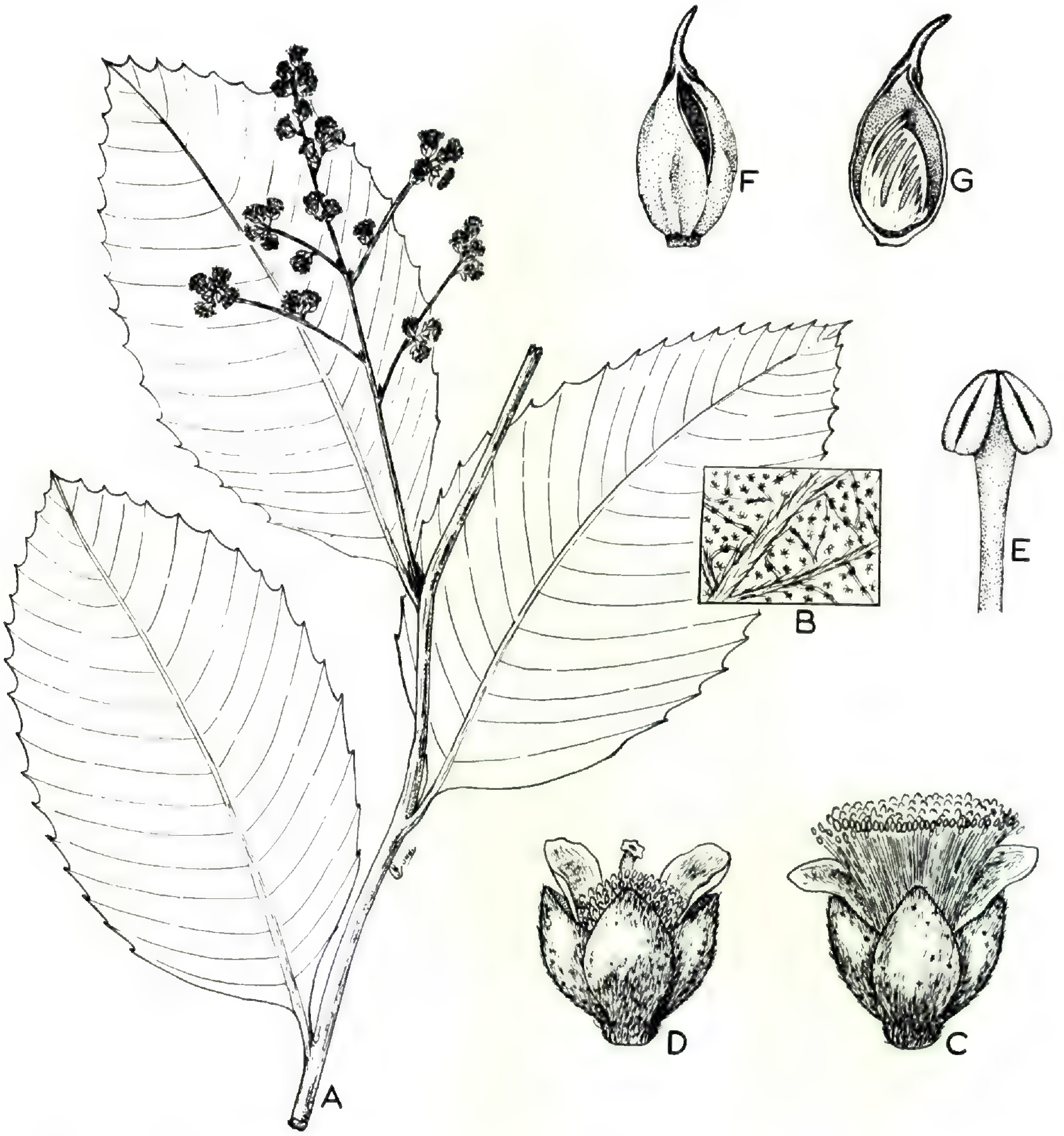

Fig. 1. TETRACERA PORTOBELLENSIS Buerling: A, flowering branch (×½); B, indumentum of lower leaf surface; C, male flower (×5); D, female flower (×5); E, upper part of filament and anther (×40); F, follicle (×3½); G, longitudinal section of follicle and arillate seed (×3½).

The first description of this genus was made under the name *Tigarea* Aubl. (Hist. Pl. Gui. Fr. 917. 1775). This name was never generally accepted and, fortunately, can be typified under *Doliocarpus* Roland.

a. Leaves smooth to slightly scabridulous, pubescent only on the veins, sepals nearly glabrous, smooth .... 1. D. multiflora
aa. Leaves scabrous above, softly pubescent beneath; sepals pubescent, scabrous .... 2. D. aspera

1. Davilla multiflora (DC.) St.-Hil., Fl. Bras. Merid. **1:** 13. 1825.

Tetracera multiflora DC., Reg. Veg. Syst. Nat. **1:** 400. 1817.
Davilla macrophylla St.-Hil., Fl. Bras. Merid. **1:** 14. 1825.
D. Sagreana Rich., Bot., Pl. Vasc. in Ramon de la Sagra, Hist. Phys. Pol. Nat. Cuba 17. 1845.
D. Matudai Lundell, Phytologia **1:** 371. 1940.
D. aspera (Aubl.) Benoist var. *Matudae* (Lundell) L. Williams, Fieldiana: Bot. **29:** 350. 1961.

Leaves with the blade elliptic to obovate, the apex shortly acuminate to obtuse, the base attenuate, the margins entire to somewhat dentate toward the apex, 7-30 cm long, 3-13 cm wide, chartaceous, smooth to slightly scabridulous, pubescent with simple hairs along the midrib above and the veins beneath, the secondary veins 8-15; petioles 10-30 mm long, narrowly alate. *Flowers* 7-12 mm broad, pedicellate; sepals broadly ovate, the inner 2 concave, to 5 mm long and wide, the outer 2-3 mm long and wide, glabrous, smooth; petals 4, obovate, 5 mm long, 3 mm wide; stamens 40-50, the filaments 5 mm long, the thecae ca 0.5 mm long, almost parallel; carpels 1, globose, the style 3 mm long, the stigma peltate. *Fruit* indehiscent to irregularly dehiscent, glabrous, to 4-5 mm in diam, the persistent style to 4 mm long.

Southern Mexico and the Antilles to northern Brazil.

canal zone: Navy Pipeline Road, *Smith & Smith 3297* (F); Frijoles, *Ebinger 94* (MO); vic of Frijoles, *Piper 5790* (US), *5793* (US), *5813* (F, US); Barro Colorado Island, *Bailey & Bailey 296* (F), *Bangham 395* (F), *Shattuck 752* (F), *Standley 41032* (US), *Wetmore & Abbe 68* (F), *184* (F), *Woodworth & Vestal 331* (F, MO), *357* (F), *485* (F); nr Fort Randolph, *Standley 28687* (US); Island in Gatun Lake, *Ostenfeld 99* (US); banks of Quebrada La Palma and Cañon of Río Chagres, *Dodge & Allen 17360* (MO); Gamboa, Navy Reservation, *A. Robyns 65-36* (MO). chiriquí: E of Gualaca, *Allen 5035* (MO). coclé: Bismarck above Penonomé, *R. S. Williams 531* (US). colón: between France Field, Canal Zone, & Catival, *Standley 30156* (US), *30284* (US). panama: San José Island, *Johnston 814* (MO, US). veraguas: Isla de Coiba, *Dwyer 2366A* (US).

The name, *D. rugosa* Poir., which has been frequently used for this species, is representative of a South American population distinct from *D. multiflora*.

2. Davilla aspera (Aubl.) Benoist, Bull. Soc. Bot. Fr. **60:** 392. 1913.—Fig. 2.

Tigarea aspera Aubl., Hist. Pl. Gui. Fr. 918, *t. 350.* 1775.
Tetracera aspera (Aubl.) Willd. in L., Sp. Pl. ed 4 [i.e. 5], **2:** 1241. 1779 (1800?).
T. Tigarea DC., Reg. Veg. Syst. Nat. **1:** 403. 1817.
Hieronia scabra Vell., Fl. Flum. 234. 1825, Fl. Flum. Ic. **5:** *t. 116.* 1835.
Davilla Kunthii St.-Hil., Pl. Us. Bras., p. 6 sub *pl. 22.* 1825, nom. subnud.
Tetracera rugosa H. B. K. ex Schlecht., Linnaea **8:** 177. 1833.
Davilla lucida Presl, Rel. Haenk. **2:** 73. 1835.

D. ovata Presl, loc. cit.
D. asperrima Splitg., Tijdschr. Nat. Gesch. Physiol. **9:** 95. 1842.
D. brasiliana Billb. ex Beurling, K. Sv. Vet.-akad. Handl. 1854: 114. 1854(?), non DC. (1817).
Delima Tigarea (DC.) Eichl. in Mart., Fl. Bras. **13**(1): 93. 1863.
Tetracera calophylla Gilg, Bot. Jahrb. **25** (Beibl. 60): 24. 1898.
Davilla pseudo-rugosa Glaziou, Bull. Soc. Bot. Fr. **52,** Mém. 3: 8. 1905.

Liana or small tree. *Leaves* with the blade elliptic to circular, the apex shortly acuminate to obtuse, the base obtuse to truncate, the margins subentire to serrulate, frequently somewhat revolute, 6-22 cm long, 4-11 cm wide, chartaceous to subcoriaceous, scabrous above with simple hairs incrusted with silica, softly pubescent beneath with simple hairs, the secondary veins 14-29; petioles 10-30 mm long, narrowly alate. *Flowers* 8-15 mm broad, pedicellate; sepals broadly ovate to cir-

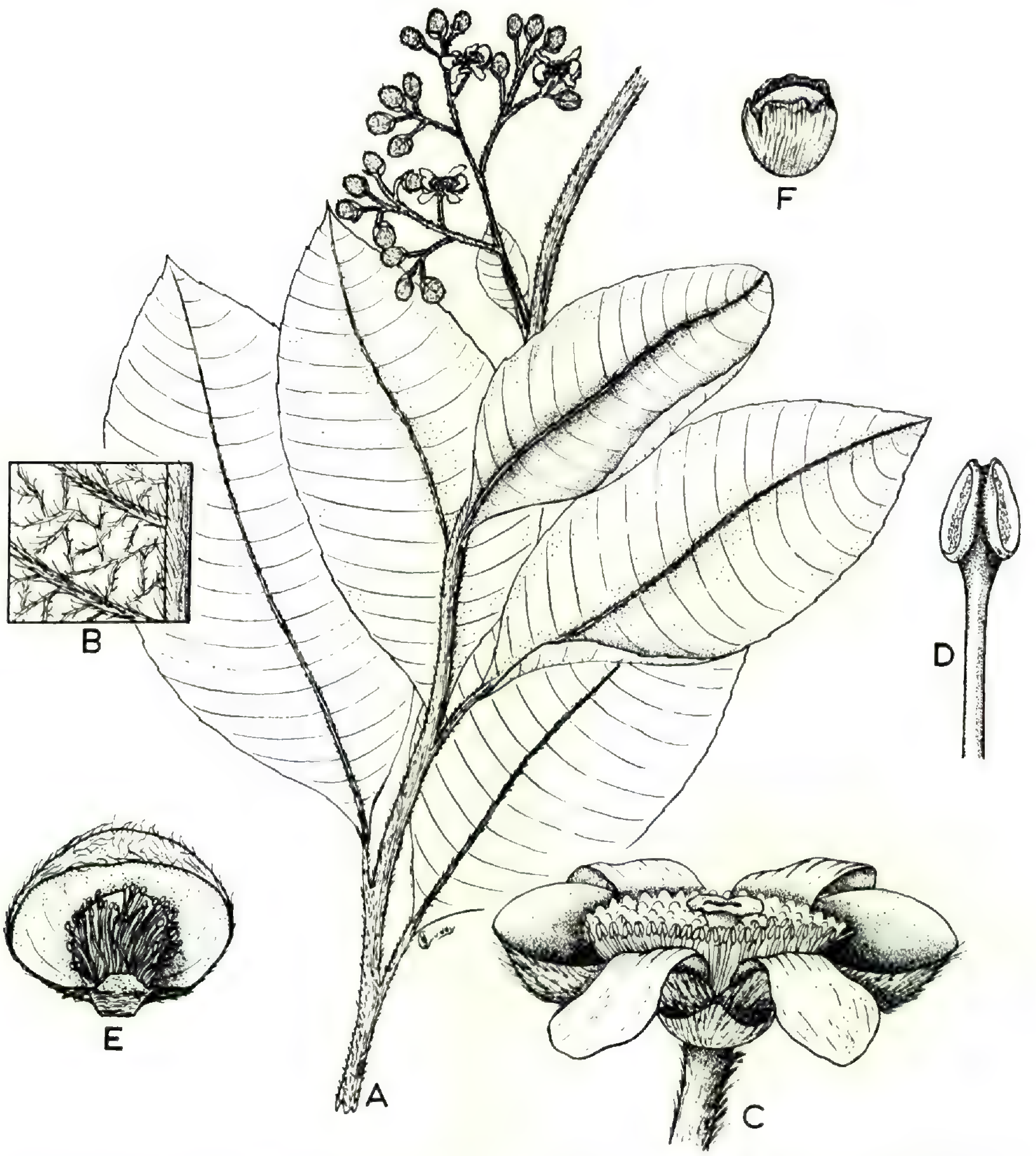

Fig. 2. DAVILLA ASPERA (Aubl.) Benoist: A, flowering branch (×½); B, indumentum of lower leaf surface; C, flower (×5); D, upper part of filament and anther (×20); E, fruit, 1 accrescent sepal removed (×3); F, arillate seed (×3½).

cular, the inner 2 concave, to 8 mm long and wide, the outer 1-3 mm long and wide, scabrous, pubescent with simple hairs; petals 4-6, yellow, obovate, 4-9 mm long, 2-5 mm wide; stamens 55-85, the filaments 3-4 mm long, the thecae ca 0.5 mm long, almost parallel; carpels 1, glabrous, the style 3 mm long, the stigma peltate. *Fruit* indehiscent to irregularly dehiscent, glabrous, to 6 mm in diam, the persistent style to 4 mm long.

Vera Cruz, Mexico and the Antilles to northern Brazil.

BOCAS DEL TORO: Cricamola valley region of Almirante, *Cooper 200* (F); Old Bank Island, vic of Chiriquí Lagoon, *von Wedel 2013* (MO), *1945* (MO). CANAL ZONE: nr Old Fort Lorenzo, mouth of Río Chagres, *Piper 5919* (US); nr beach at Ft. Kobbe, *Duke 4210* (MO); Gatun, *Hayes 5* (US); Gatun Station, *Hayes s.n.* (F, MO, US); Ancon Hill, *Bro. Celestine 68* (US), *Duke 4609* (MO), *J. & M. Greenman 5101* (MO), *Killip 12104* (US), *Pittier s.n.* (US), *R. S. Williams 39* (US); between Corozal and Ancon, *Pittier 2643* (US); Balboa Heights, *J. & M. Greenman 5068* (MO); Albrook, *Dwyer & A. Robyns 178* (MO); Las Cruces Trail, *Hunter & Allen 703* (MO); Chagres, *Fendler 26* (MO, US); vic Miraflores Lake, *P. & G. White 54* (MO); Fort Sherman, *Dwyer & A. Robyns 39* (MO), *Standley 31074* (US); Ft. Kobbe, *Duke 3956* (MO); vic of Summit, *Standley 30073* (US). CHIRIQUÍ: Sabana de El Boquete, *Pittier 3325* (US). COCLÉ: Aguadulce, *Pittier 4984* (US); between Las Margaritas and El Valle, *Woodson et al. 1292* (MO, US); hills S of El Valle de Antón, *Allen 2529* (US). COLÓN: between France Field, Canal Zone, and Catival, *Standley 30167* (US), *30185* (US). DARIEN: vic of La Palma, *Pittier 5480* (US). HERRERA: vic of Ocú, *Allen 4055* (MO). PANAMA: vic of Bella Vista, *Piper 5382* (F, US); vic of Juan Franco Race Track, nr Panama City, *Standley 27743* (US); nr Pacora River, *Miller 1786* (US); Las Sabanas, *Standley 25852* (US), *25874* (US); between Las Sabanas & Matías Hernández, *Standley 31821* (US); nr Punta Paitilla, *Standley 26279* (US); San José Island, *Erlanson 12* (US), *Johnston 625* (US); Río Tocumen, *Standley 29487* (US); Tumba Muerto Rd., nr Panama City, *Standley 29746* (US); Cerro Azul, *Ebinger 413* (MO); Savanas, *Macbride 2636* (F, US); Taboga Island, *Bro. Celestine 51* (US), *Standley 27996* (US), *Miller 1838* (US), *Allen 114* (F, MO, US), *Dwyer 2181* (MO); Cerro Campana, *Ebinger 373* (MO). VERAGUAS: trail between Cañazas & foot of the Cordillera Central, headwaters of Río Cañazas, *Allen 206* (F, MO). PROVINCE UNKNOWN: *Anderson s.n.* (US).

I have seen the type specimen of *D. aspera* (Aubl.) Benoist and I am certain of its identity with the Central American population. With its scabrous sepals and silica incrusted leaves, which are used like sandpaper by the populace of British Honduras, it is easily distinguished from the smoother *D. multiflora* (DC.) St.-Hil.

3. CURATELLA Loefl.

Curatella Loefl., Iter Hisp. 260. 1758.

Trees, small, or shrubs. *Leaves* alternate, coriaceous, scabrous, pubescent with stellate hairs, rarely stellate and simple hairs mixed, incrusted with silica, the petioles canaliculate, alate. *Inflorescences* arising in the axils of fallen leaves on old wood, rarely terminal on the young branches, paniculiform, many-flowered. *Flowers* perfect, actinomorphic; sepals 4-5, persistent, more or less equal; petals 4-5, free, caducous; stamens indefinite, persistent, the filaments free, filiform, the anthers longitudinally dehiscent, 2-thecate, the thecae nearly parallel, about half sunken into the dilated connective; carpels 2, rarely 1 or 5, globose, pilose, fused basally, 1-thecate, the ovules 2, erect, basal, the styles filiform, the stigmas pelate. *Fruit* usually bilobed, globose, pilose, fused basally, dehiscent along the ventral and

lateral sutures into 4 valves, the carpels each with 2, rarely 1 seeds, the seeds smooth, arillate, the aril more or less entire, nearly enveloping the seed at maturity, the embryo small.

One species restricted to the American tropics.

Pinzona Mart. & Zucc. (Akad. Wiss. Munich, Math.-Naturwiss. Abt., Abhandl. **1:** 371. 1832), often given as a synonym for *Curatella,* is based on a plant which has the expanded inflorescence and bicarpellate ovary of *Curatella* and the lianous habit of *Doliocarpus.* Following Gilg's treatment (Nat. Pfanzenfam. **3**(6): 114. 1893), *Pinzona* is included in the synonymy of the latter.

1. CURATELLA AMERICANA L., Syst. Nat. ed. 10, 1079. 1759.—Fig. 3.

C. cambaiba St.-Hil., Pl. Us. Bras. *pl. 24.* 1825
C. Grisebachiana Eichl. in Mart., Fl. Bras. **13**(1): 69. 1863.
C. americana var. *pentagyna* J. D. Sm., Bot. Gaz. **46:** 109. 1908.

Shrub or small tree. *Leaves* with the blade elliptic to ovate, the apex rounded to retuse, the base obtuse to truncate, the margins repand, 8-18 cm long, 5-9 cm wide, coriaceous, pustulate, scabrous, stellate-pubescent, the secondary veins 10-20; petioles 5-20 mm long, narrowly alate. *Flowers* 7-12 mm broad, pedicellate; sepals obovate, 5-7 mm long, 3-5 mm wide, pubescent within and without; petals white to greenish, obovate, 5-7 mm long, 3-5 mm wide; stamens 60-80, the filaments 6-8 mm long, the thecae 0.7 mm long, nearly parallel; carpels 2, globose, pubescent with simple hairs, the styles filiform, 3 mm long, the stigmas peltate. *Fruit* pubescent with simple hairs.

Southern Mexico to Bolivia and northern Brazil.

CANAL ZONE: vic of Summit, *Standley 30108* (US); Chiva-Chiva Trail, Red Tank to Pueblo Nuevo, *Piper 5715* (US); Río Agua Salud, nr Frijoles, *Piper 5868* (US). CHIRIQUÍ: between Boquete and David, *Pittier 3303* (US). COCLÉ: between Porto Posado & Penonomé, *R. S. Williams 160* (US); llanos outside of Penonomé, *Ebinger 1002* (MO). PANAMA: between Matías Hernández & Juan Díaz, *Standley 32081* (US); vic of Juan Franco Race Track, nr Panama City, *Standley 27770* (US); San José Island, *Johnston 575* (US); nr Bejuco, *Miller 1792* (US); Taboga Island, *Macbride 2825* (F), *Standley 28009* (US); Río Las Lajas, *Allen 1615* (MO); Sabana, nr Chepo, *Hunter & Allen 71* (MO); along road to Río Pacora, *Allen 816* (F, MO); on sabana, road to Chepo, *Hunter & Steyermark s.n.* (MO). VERAGUAS: trail between Cañazas & foot of the Cordillera Central, headwaters of Río Cañazas, *Allen 198* (F, MO). PROVINCE UNKNOWN: *Haenke s.n.* (MO).

The leaves of *Curatella,* which are heavily incrusted with silica, are used by the Central Americans as a substitute for sandpaper. *C. americana* is frequently found in the savannas in association with *Anacardium occidentale* L.

4. DOLIOCARPUS Roland.

DOLIOCARPUS Roland., K. Sv. Vet.-akad. Handl. 1756: 249. 1756(?).

Soramia Aubl., Hist. Pl. Gui. Fr. 552, *t. 219.* 1775.
Calinea Aubl., loc. cit. 556, *t. 221.*
Tigarea Aubl., loc. cit. 917, *t. 350.*
Rhinium Schreb. in L., Gen. Pl. ed. 8, 701. 1791.
Mappia Schreb. loc. cit. 806, non Jacq. (1797).
Othlis Schott ex Spreng. in L., Syst. Veg. ed. 16, **4**(2): 407. 1827.

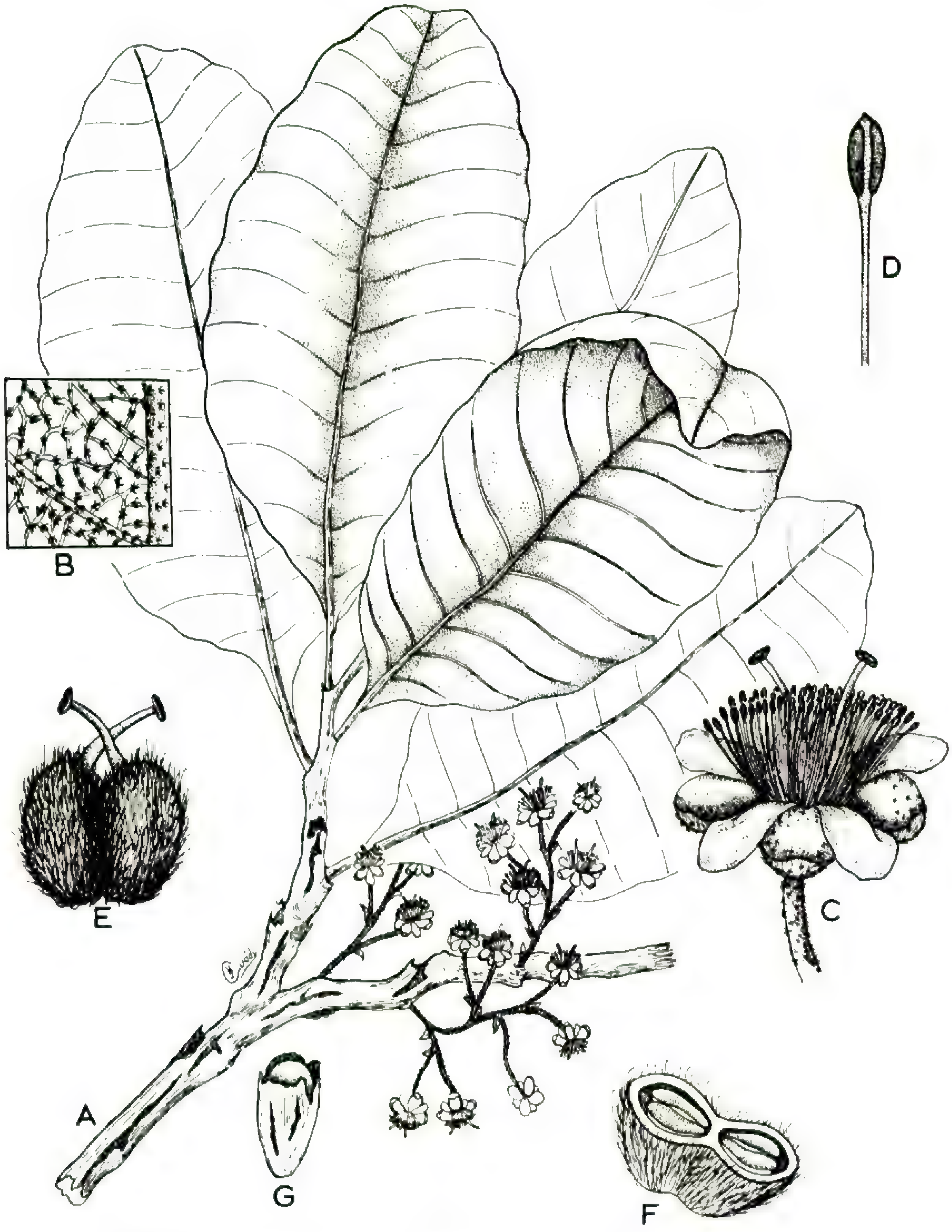

Fig. 3. Curatella americana L.: A, flowering branch (×½); B, indumentum of lower leaf surface; C, flower (×3½); D, upper part of filament and anther (×10); E, fruit (×2½); F, fruit, cross-section (×3); G, arillate seed (×3½).

Pinzona Mart. & Zucc., Akad. Wiss. Munich, Math.-Naturwiss. Abt., Abhandl. **1:** 371. 1832.
Ricaurtea Triana, Ann. Sci. Nat., Bot., sér. 4, **9:** 47. 1858.

Lianas or scandent shrubs. *Leaves* alternate, smooth, pubescent with simple hairs only, the petioles canaliculate, narrowly alate. *Inflorescences* axillary, obscurely glomerulate. *Flowers* perfect, actinomorphic; sepals 3-6, mostly 5, caducous; stamens indefinite, persistent, the filaments free, filiform, the anthers longitudinally dehiscent, 2-thecate, the thecae parallel or basally divergent, about half sunken into

the dilated connective; carpels 1, rarely 2, globose, the ovules 2, erect, basal, the styles filiform, the stigmas simple to peltate. *Fruit* berry-like or follicular and dehiscent along the ventral suture across the apex, each carpel maturing 2, rarely 1 seeds; seeds smooth, arillate, the aril more or less entire, surrounding the seed at maturity, the embryo small.

Several species in the American tropics.

a. Ovary and fruit pubescent, the style 4-8 mm long, sometimes exceeding the sepals; sepals sericeous within.
  b. Leaves punctate; pedicels 5-20 mm long .... 1. D. MAJOR
  bb. Leaves not punctate; pedicels 2-4 mm long .... 2. D. OLIVACEUS
aa. Ovary and fruit glabrous to slightly pubescent, the style 1-2 mm long, not exceeding the sepals; sepals glabrous to slightly pubescent within.
  c. Inflorescence glomerulate; petioles 5-15 mm long .... 3. D. DENTATUS
  cc. Inflorescence in fascicles of few-flowered cincinni; petioles 20-30 mm long .... 4. D. GUIANENSIS

Doliocarpus coriaceus (Mart. & Zucc.) Gilg, with which the Antillean *D. callineoides* (Eichl.) Gilg is synonymous, has been collected in Nicaragua and Guatemala and may occur in Panama. It is easily distinguished by its bicarpellate ovary and its paniculate inflorescence.

1. DOLIOCARPUS MAJOR Gmel. in L., Syst. Nat. ed 13, **2**: 805. 1791.

D. Rolandri Gmel., loc. cit.
Tetracera stricta Willd. in L., Sp. Pl. ed. 4 [i.e. 5], **2**: 1241. 1799 (1800?).
T. doliocarpus Willd., loc. cit.
Doliocarpus scandens Poir. in Lam., Encycl. Méth. Bot. Suppl. **2**: 499. 1812.
D. strictus Poir., loc. cit. 500.
Delima guianensis Rich. ex DC., Reg. Veg. Syst. Nat. **1**: 408. 1817.
Doliocarpus dentosus Mart., Flora **24**(2) (Beibl.): 65. 1841.
D. spinulifer Miq., Linnaea **18**: 266. 1844.
D. brevipedicellatus Garcke, Linnaea **22**: 47. 1849.
D. punctatus Standley, J. Wash. Acad. Sci. **15**: 286. 1925.

Liana. *Leaves* with the blade elliptic to obovate, the apex acuminate, the base obtuse, the margins entire to serrate, 7-15 cm long, 2-8 cm wide, chartaceous, punctate, the puncti with a short simple hair arising from the center, the blades otherwise glabrous or pubescent with scattered simple hairs along the midvein above and the major veins beneath, the secondary veins 6-12; petioles 5-15 mm long, narrowly alate. *Inflorescence* axillary, fascicled. *Flowers* 20-30 mm broad, the pedicels 5-12 mm long at anthesis, to 10-20 mm long in fruit; sepals 4-5, broadly ovate, 3-6 mm long and wide, pubescent within and without; petals 2, white to pale yellow, obovate to obdeltoid, 15 mm long, 10 mm wide; stamens 75, deciduous, the filaments filiform, 5-7 mm long, the thecae 0.7 mm long, nearly parallel; carpels 1, pubescent, globose, the styles 6-8 mm long, the stigmas simple. *Fruit* berry-like and indehiscent or dehiscing across the apex, pubescent, globose.

Panama to northern Brazil.

BOCAS DEL TORO: Nances Cay, vic of Chiriquí Lagoon, *von Wedel 2860* (F, MO); s. loc., *von Wedel 446* (F, MO). CANAL ZONE: Agua Clara, *Pittier 3988* (US); Frijoles, *Ebinger 317* (MO); vic of Gatun Lake S of island, *P. White 127* (F, MO); vic of Miraflores, *G. White 132* (F, MO); coast road 2 mi NE of Piña Valley, NW part of Canal Zone (area W of Limón Bay, Gatun Locks & Gatun Lake), *Johnston 1526* (MO); Gatun, *Hayes s.n.* (MO),

22(US); Gatun Lake, *Bangham 438* (US); Chagres, *Fendler 305* (MO); Barro Colorado Island, *Shattuck 623* (US), 1075 (US), *Standley 41059* (US); Coco Solo Weather Station, *Duke 4272* (MO). COLÓN: between France Field, Canal Zone, & Catival, *Standley 30173* (F, US), *30323* (US); France Field, *Stevens 1337* (US); along Río Fató, *Pittier 3949* (US), *4187* (US). DARIEN: vic of Campamento Bueno Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 837* (MO), *844* (MO); trail, Paya to Pucra, vic of Paya, Río Paya, *Stern et al. 223* (MO); along Río Tuira below El Real & Piriaque Island, *Stern et al. 899* (MO). PANAMA: Río Pita, 1-3 mi above confluence with Río Maestra, *Duke 4780* (MO); ca 6 mi E of Chepo on Pan-Am. Highway, *Duke 4067* (MO). SAN BLAS: high hills back of Puerto Obaldía, San Blas coast, *Pittier 4339* (US); forests around Puerto Obaldía, *Pittier s.n.* (US).

2. Doliocarpus olivaceus Sprague & Williams ex Standley, Contr. U.S. Nat. Herb. **27:** 265. 1928, nom. nud. in clavi; ex Kenoyer & Standley, Field Mus. Nat. Hist., Publ. Bot., ser. **4:** 152. 1929, nom. subnud.; ex Standley, Contr. Arnold Arb. **5:** 105. 1933, nom. subnud.—Fig. 4.

Frutex scandens. *Folia* elliptica apice acuminata basi obtusa marginibus leviter repandis obscureque dentatis vel subintegris 13-22 cm longa 5-9 cm lata subcoriacea glabra nervis lateralibus 8-11 petiolo 15-30 mm longo anguste alato. *Inflorescentia* cauliflora fasciculataque. *Flores* 10 mm lati pedicellis 2-4 mm longis; sepala 4-6 ovata 2-5 mm longa 2-5 mm lata intus sparse pubescentia extusque glabra; petala 4-5 obovata ca 6 mm longa et lata; stamina 35-45 decidua filamentis filiformibus 7 mm longis et thecis 0.7 mm longis fereque parallelis; carpellum 1 pubescens globosum stylis 4-5 mm longis et stigmatibus peltatis. *Fructus* indehiscens pubescens globosus.

Known only from Panama.

CANAL ZONE: Road K-9, along Cocoli River, *Stern et al. 11* (MO); Barro Colorado Island, *Stevens 18* (US), *Kenoyer 608* (US), *616* (US), *Shattuck 915* (US). PANAMA: along Pan-Am. Highway, open grazed area nr Jenine, Río Canita, *Duke 3891* (MO); nr Tapía River, Juan Díaz region, *Maxon & Harvey 6746* (US, lectotype); Río Tapía, *Standley 26221* (US).

Standley & Kenoyer give meager and conflicting descriptions of *D. olivaceus* in the references cited above; furthermore, no specimen is cited. This Latin diagnosis is offered with the hope that it may contribute to a better understanding of the species.

The Maxon & Harvey specimen is from the U.S. National Herbarium and was annotated "isotype" by Sprague in 1926. It is, undoubtedly, the specimen on which Standley based the species.

Doliocarpus olivaceus differs from *D. major* in the nonpunctate leaves, the nearly sessile flowers and the tendency toward cauliflory.

3. Doliocarpus dentatus (Aubl.) Standley, J. Wash. Acad. Sci. **15:** 286. 1925.

Tigarea dentata Aubl., Hist. Pl. Gui. Fr. 920, *t. 351*. 1775.
Tetracera tomentosa Willd. in L., Sp. Pl. ed. 4 [i.e. 5], **2:** 1241. 1799 (1800?).
T. cuspidata G. F. W. Meyer, Prim. Fl. Essequeboensis 205. 1818.
Delima tomentosa E. H. F. Meyer, Nov. Acta Acad. Leop.-Carol. **12:** 816. 1825.
Doliocarpus pubens Mart., Flora **21**(2) (Beibl.): 49. 1838.
D. semidentatus Garcke, Linnaea **22:** 48. 1849.
Delima dasyphylla Miq., Stirp. Surin. Select. 107. 1850 (cf. Natuurk. Verh. Hollands. Maatsch. Wet. Haarlem, ser. 2, **7.** 1851).

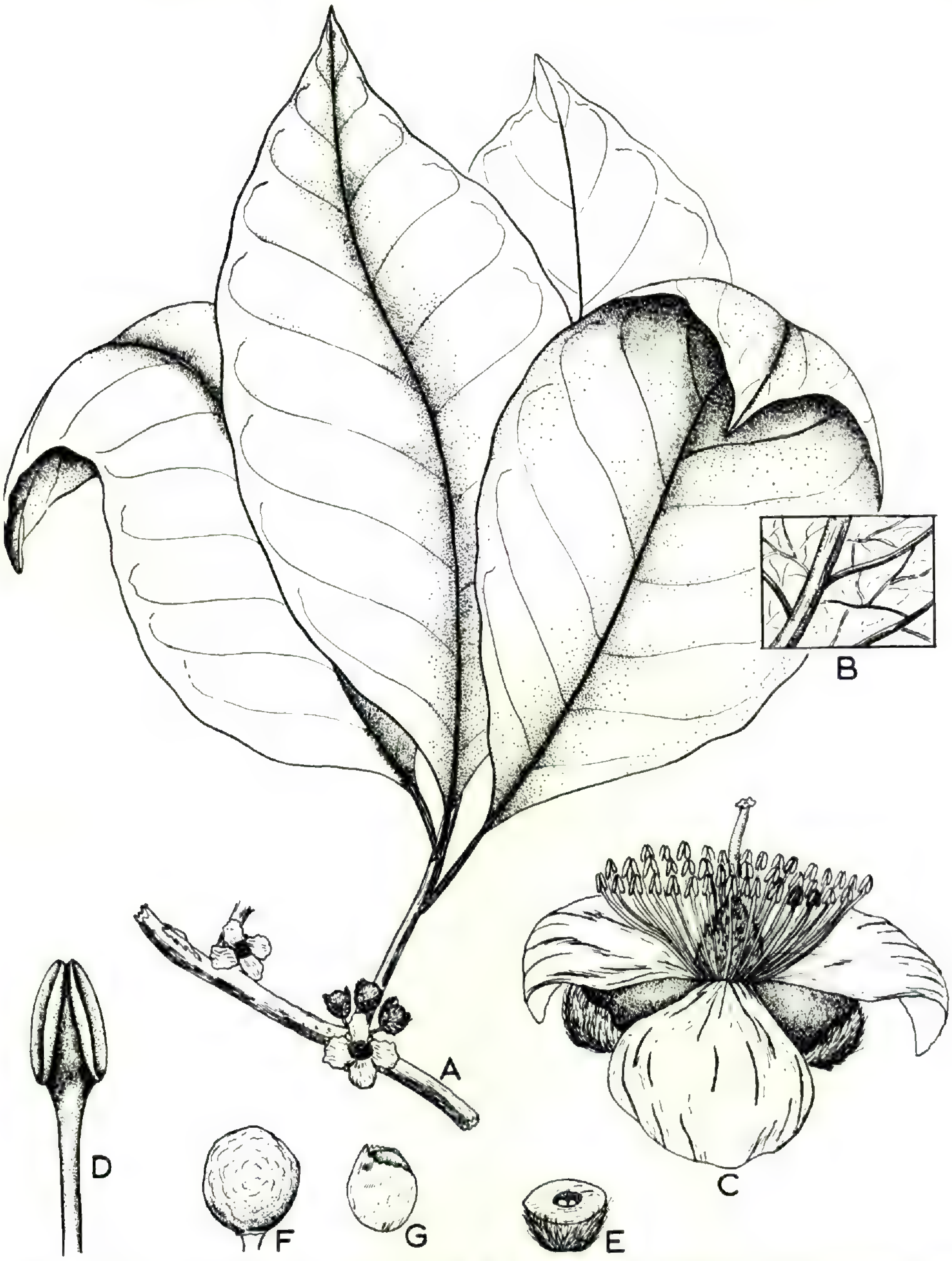

Fig. 4. Doliocarpus olivaceus Sprague & Williams ex Standley: A, flowering branch (×½); B, indumentum of lower leaf surface; C, flower (×5); D, upper part of filament and anther (×20); E, ovary, cross-section (×5); F, fruit (×1); G, arillate seed (×1⅓).

Doliocarpus oaxacanus Szyszyl., Pugill. Pl. Nov. Am. Centr. Merid. 1. 1894.
Curatella Glaziovii Gilg, Bot. Jahrb. **25** (Beibl. 60): 25. 1898.
C. Glazioviana Gilg, Bull. Soc. Bot. Fr. **52**, Mém. 3: 9. 1905.

Liana or scandent shrub. *Leaves* with the blade elliptic, the apex acuminate to rounded, the base obtuse, the margins entire to dentate, 8-20 cm long, 3-7 cm wide, chartaceous to subcoriaceous, glabrous to slightly pubescent with simple hairs along the veins beneath, the secondary veins 6-13; petioles 5-15 mm long, narrowly alate. *Inflorescence* cauliflorous or axillary, glomerulate. *Flowers* 5-8 mm broad, the pedicels 5-10 mm long at anthesis, to 20-25 mm long in fruit;

sepals 3-5, obovate, 2-4 mm long, 2-3 mm wide, glabrous to slightly pubescent within, slightly pubescent without; petals 2-4, white, spatulate to obovate, 4-5 mm long, 2-4 mm wide; stamens 30-45, deciduous, the filaments filiform, 4-5 mm long, the thecae 0.5 mm long, nearly parallel; carpels 1, glabrous, globose, the style terete, 1.0-1.5 mm long, the stigma peltate. *Fruit* indehiscent, glabrous, globose.

British Honduras and the Antilles to Bolivia and northern Brazil.

CANAL ZONE: Albrook, *Dwyer & A. Robyns 177* (MO); Ancon Hill, *Pittier s.n.* (US); Fort Sherman, *Maxon & Valentine 6971* (US); between Tumba Vieja & Salamanca, *Steyermark & Allen 16756a* (MO). COCLÉ: Penonomé & vic, *R. S. Williams 272* (US); S of El Valle de Antón, *Allen 2528* (MO); mountains beyond La Pintada, *Hunter & Allen 630* (US). DARIEN: vic of Caná, *Stern et al. 549* (MO). PANAMA: Río Las Lajas, *Allen 1617* (MO); between Matías Hernandez & Juan Díaz, *Standley 32071* (US); San José Island, *Erlanson 44, 79* (US), *Johnston 520* (MO), *564* (US); Trapiche Island, *Miller 1889* (US).

4. Doliocarpus guianensis (Aubl.) Gilg in Engl. & Prantl, Nat. Pflanzenfam. **3**(6): 114. 1893.

Soramia guianensis Aubl., Hist. Pl. Gui. Fr. 552. *t. 219.* 1775.
Tetracera obovata Willd. in L., Sp. Pl. ed. 4 [i.e. 5], **2:** 1241. 1799 (1800?).
Doliocarpus soramia DC., Reg. Veg. Syst. Nat. **1:** 406. 1817.
D. multiflorus Standley, J. Wash. Acad. Sci. **15:** 285. 1925.

Liana. Leaves with the blade elliptic to obovate, the apex shortly acuminate, the base obtuse, the margins entire to somewhat dentate toward the apex, 10-25 cm long, 5-10 cm wide, subcoriaceous, glabrous, the secondary veins 6-9; petioles 20-30 mm long, narrowly alate. *Inflorescence* cauliflorous or axillary, composed of few-flowered cincinni in fascicles. *Flowers* 7-9 mm broad, the pedicels 2-10 mm long; sepals 5, oblong to obovate, 5-6 mm long, 2-4 mm wide, glabrous to slightly pubescent within and without; petals 3-4, white, obovate, 3-4 mm long, 2-3 mm wide; stamens 65-80, persistent, the filaments filiform, 5 mm long, the thecae 0.5 mm long, nearly parallel; carpels 1, glabrous to slightly pubescent, the styles terete, 1-2 mm long, the stigma peltate. *Fruit* dehiscent across the apex or indehiscent, glabrous to slightly pubescent, globose.

British Honduras to French Guiana.

CANAL ZONE: Chagres, *Fendler 50* (MO). COLÓN: between France Field, Canal Zone, & Catival, *Standley 30285* (US).

Doliocarpus guianensis, close to *D. dentatus,* can be distinguished from it and the other two species occuring in Panama by its expanded inflorescences.

5. SAURAUIA Willd.

Saurauia Willd., Ges. Naturf. Freunde Neue Berlin Schr. **3:** 407. 1801.

Palaua Ruiz & Pavon, Fl. Peruv. Chil. Prodr. 100. 1794, non Cav. (1785).
Apatelia DC., Mém. Soc. Phys. Hist. Nat. Genève **1:** 426. 1822.
Marumia Reinw. ex Blume, Cat. Gew. Buitenz. 79. 1823, nom. nud.
Reinwardtia Blume ex Nees, Syll. Pl. Nov. (Ratisb.) **1:** 96. 1824, non Dumort. (1722), Korth (1841) nec Spreng. (1825).
Tonshia Buch.-Ham. ex D. Don, Prodr. Fl. Nep. 225. 1825.
Blumia Spreng. in L., Syst. Veg. ed. 16, **3:** 126. 1826, non Nees (1823).

Obelanthera Turcz., Bull. Soc. Nat. Moscou **20**(1): 148. 1847.
Draytonia A. Gray, Bot., Phanerog. in U. S. Expl. Exped. (1838-42) **15**: 206. 1854.
Trematanthera F. Muell., Vict. Nat. **3**: 71. 1886.

Trees and shrubs, pubescent. *Leaves* simple, spiral, petiolate. *Inflorescences* axillary, basically thyrisiform. *Flowers* regular, basically 5-merous (*S. laevigata* basically 4-merous), pedicellate; sepals 3-6, often 5, persistent, the outer usually somewhat smaller and more densely pubescent than the inner, the aestivation quincuncial; petals 3-6, usually 5, white to pinkish, fused at the base, falling as a unit with the stamens; stamens indefinite, the filament adnate to the base of the corolla, filiform, pubescent at the base, the anthers bifurcate, versatile, extrorse, basally dehiscent by rimiform pores; ovary globose, 3- to 6-, frequently 5-locular and sulcate, the ovules indefinite, anatropous, the placentation axile, the styles as many as the locules, free, filiform, obsolete to exceeding the stamens, the stigmas simple to capitate. *Fruit* baccate, the seeds many, small, areolate, embedded in a mucilaginous pulp, the embryo straight, ⅓-½ as long as the seed; endosperm mealy.

Numerous species in the tropics of Asia and America.

Saurauia has been treated as a member of the *Theaceae, Actinidiaceae, Saurauiaceae* and *Dilleniaceae.* It is my opinion that the genus is most closely allied with *Clethraceae;* however, as a matter of expediency, following the Englerian classification, it is included in the *Dilleniaceae.*

a. Plants often copiously pubescent; leaves with tertiary veins elevated, more prominent than the lesser reticulation; flowers usually 5-merous, more than 12 mm broad, the sepals densely pubescent.
 b. Leaves smooth above; ovary and fruit densely pubescent .... 1. S. VERAGUASENSIS
 bb. Leaves scabridulous above; ovary and fruit glabrous .... 2. S. RUBIFORMIS
aa. Plants sparingly pubescent; leaves with tertiary veins immersed, scarcely more prominent than the lesser reticulation; flowers 3- to 5-merous, sometimes less than 10 mm broad; ovary and fruit glabrous.
 c. Flowers 4-, rarely 5- or 3-merous, less than 10 mm broad, the sepals sparingly pubescent .... 3. S. LAEVIGATA
 cc. Flowers 5-merous, more than 12 mm broad, the sepals densely pubescent .... 4. S. SEIBERTII

1. SAURAUIA VERAGUASENSIS Seem., Bot. Voy. Herald 249. 1854.

S. montana Seem., loc. cit. 87, *t. 16.* 1853.
S. costaricensis J. D. Sm., Bot. Gaz. **23**: 236. 1897.
S. ovalifolia J. D. Sm., loc. cit. **42**: 292. 1906.
S. costaricensis var. *brachitricha* Buscalioni, Malpighia **27**: 12. 1914-1915.
S. costaricensis var. *dolicotricha* Buscalioni, loc. cit. 15.
S. pseudocostaricensis Buscalioni, loc. cit. 25.
S. pseudoveraguensis Buscalioni, loc. cit. 30.
S. Engleriana Buscalioni, loc. cit. 131. 1915-1916.
S. setosa Standley, Field Mus. Nat. Hist., Bot. Ser., **18**: 693. 1937.

Shrub or tree to 15 m, copiously pubescent. *Leaves* with the blade narrowly elliptic to obovate, the apex acute to acuminate, the base obtuse to acute, frequently oblique, the margins setaceous-serrulate to serrate, 11-40 cm long, 3-18 cm wide, chartaceous to subcoriaceous, the secondary veins in 14-26 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, sparingly to abundantly

strigillose, sericeous, setulose or hirtellous between the veins above, usually stellate or dendroid between the veins beneath, the axils of the secondary veins frequently villous-barbate beneath; petioles 1-9 cm long, 2-4 mm in diam. *Inflorescence* 7- to 95-flowered, 7-30 cm long, 3-18 cm wide, the primary peduncle 4-10 cm long, the bracts foliaceous or linear to triangular, 1-50 mm long. *Flowers* 13-27 mm broad, the buds to 5-8 mm in diam, the pedicels 3-10 mm long; sepals 5, 4-7 mm long, 3-7 mm wide, the inner 2 medially densely heterotrichous, laterally appressed-stellate, submarginally glabrous, ciliate, the imbricate sepal densely heterotrichous on the exterior half, appressed-stellate, submarginally glabrous, ciliate on the interior half, the outer 2 densely heterotrichous, all submarginally appressed-stellate, glabrous elsewhere within; petals 5, white to pinkish, oblong to obovate, 7-11 mm long, 4-9 mm wide, obtuse to retuse; stamens 23-48, the anthers 1.5-2.5 mm long, the filaments 1.5-3.0 mm long; ovary 5-locular, globose, densely pubescent with filiform trichomes, the styles obsolete or up to 4 mm long, the stigmas simple to subcapitate. *Berries* 6-10 mm in diam, globose, densely pubescent with filiform trichomes.

Honduras, Costa Rica and Panama.

CHIRIQUÍ: Bajo Chorro, *Davidson 190* (A, F, MO); Bajo Mona & Quebrada Chiquero, *Woodson & Schery 521* (GH, MO, US); trail from Bambito to Cerro Punta, *Allen 314* (A, F, GH, MO, US); vic of Boquete, *Allen 4650* (MO), *Bro. Maurice 698* (GH, US), *Maxon 4932* (US), *Pittier 2874* (F, US), *2942* (F, US); Volcán Chiriquí, *Davidson 979* (A, F, MO, US), *Seeman 1235* (K); Cerro Horqueta, *C. & W. von Hagen 2052* (MO); vic of Monte Lirio, valley of the upper Río Chiriquí Viejo, *Seibert 303* (F, MO); Río Chiriquí Viejo valley, between El Volcán & Cerro Punta, *G. White 3* (F, GH, MO); valley of the upper Río Chiriquí Viejo, *P. White 24* (MO); Río Chiriquí Viejo valley, nr El Volcán, *P. White 188* (MO, US); Casita Alta, Volcán Chiriquí, *Woodson et al. 809* (A, F, MO); vic of New Switzerland, central valley Río Chiriquí Viejo, *Allen 1356* (GH, MO, US).

Specimens of this population have usually been identified as *S. costaricensis*, probably because of J. Donnell Smith's numerous collections in Costa Rica and because Buscalioni, in his monograph of the American species of *Saurauia*, never recognized the name *S. veraguasensis*. Instead, he recognized Smith's epithet and published a new name, *S. pseudoveraguensis*, citing only Seemann's type collection.

2. SAURAUIA RUBIFORMIS Vatke, Linnaea **40:** 221. 1876.

S. sarapiquensis Carrière, Rev. Hort. **49:** 60. 1877.
S. polyantha Gilg in Engl. & Prantl, Nat. Pflanzenfam. **3**(6): 128, *fig. 67 (A-J)*. 1893.
S. rubiformis f. *Veranii* Buscalioni, Malpighia **27:** 144. 1915-1916.
S. rubiformis f. *aspera* Buscalioni, loc. cit. 145.
S. pseudorubiformis Buscalioni, loc. cit. 149.
S. pseudorubiformis var. *guatemalensis* Buscalioni, loc. cit. 155.

Shrub or multiple-trunked tree to 15 m, copiously pubescent. *Leaves* with the blade broadly to narrowly obovate to elliptic, the apex shortly acuminate to acute, rarely obtuse, the base obtuse, rarely acute or cordate, the margins serrulate, 13-30 cm long, 4-16 cm wide, chartaceous to subcoriaceous, the secondary veins 15-25 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, scabridulous with trichomes usually shorter than 1 mm between the veins above, sparingly to abundantly tufted-, clustered-, or stellate-pubescent between the veins beneath; petioles ca 1.5-7.0 cm long, 2-4 mm in diam. *Inflorescence* 15- to 55-,

rarely 190-flowered, 15-25, rarely to 33 cm long, 4-10, rarely to 18 cm wide, the primary peduncle 5-16 cm long, the bracts linear, triangular to foliaceous, 2-30 mm long. *Flowers* 15-30 mm broad, the buds to 5-8 mm in diam, the pedicels 3-25 mm long; sepals 5, 4-8 mm long, 4-6 mm wide, the pubescence usually shorter than 1 mm, the inner 2 medially densely heterotrichous, laterally densely clustered-pubescent, the imbricate sepal densely heterotrichous on the exterior half, densely clustered-pubescent on the interior half, the outer 2 densely heterotrichous, all densely clustered-pubescent within; petals 5, white, oblong, 6-12 mm long, 3-7 mm wide, obtuse to incised at the apex; stamens 26-41, the filaments 2-3 mm long, the anthers 2-3 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the styles obsolete to 4 mm, the stigmas simple. *Fruit* not seen.

Guatemala, Costa Rica and Panama.

CHIRIQUÍ: Casita Alta, *Woodson et al. 957* (MO); W slopes of Cerro Horqueta, *Allen 4797* (MO); nr Cerro Punta, *Stern & Chambers 84* (US); Quebrada Velo, *Allen 4671* (F, MO), *Woodson & Schery 263* (MO, US).

Saurauia rubiformis is closely allied with *S. Seibertii* Standley. They are similar in the distribution of the pubescence of the sepals and in the kinds of trichomes, including clustered and tufted types, making up the pubescence of both sepals and leaves. *Saurauia rubiformis* may be distinguished from the latter by its larger, more densely pubescent leaves.

3. SAURAUIA LAEVIGATA Triana & Planchon, Ann. Sci. Nat., Bot., sér. 4, **18:** 267. 1862.

S. Yasicae Loesener, Bot. Jahrb. **23:** 125. 1896.
S. Herbert-Smithii Rusby, Descr. New Sp. S. Am. 57. 1920.
S. leucocarpa Schlecht. var. *Smithiana* Buscalioni, Malpighia **29:** 232. 1922.
S. Yasicae var. *laevigata* Buscalioni, loc. cit. 366.
S. Yasicae var. *laevigata* f. *Veranii* Buscalioni, loc. cit. 413. 1923.
S. Smithiana Buscalioni, loc. cit. 445.
S. pseudopittieri Buscalioni, loc. cit. **30:** 97. 1927.
S. Zetekiana Standley, J. Arnold Arb. **11:** 124. 1930; Contr. Arnold Arb. **5:** 105. 1933.
S. belizensis Lundell, Field Lab. **13:** 7. 1945.

Tree to 30 m, sparingly pubescent. *Leaves* with the blade obovate to elliptic, the apex obtuse to acuminate, the base subattenuate to obtuse, sometimes oblique, the margins serrulate to serrate, 6-22 cm long, 2-10 cm wide, membranous to chartaceous, the secondary veins 7-14, rarely 18 pairs, the tertiary veins immersed, scarcely more prominent than the lesser reticulation, the epidermis pustulate, glabrous between the scattered-tufted veins above and beneath; petioles 0.5-3.0 cm long, 0.5-2.5 mm in diam. *Inflorescence* 40- to more than 150-flowered, 5-20 cm long, 2-10 cm wide, the primary peduncles 2-10 cm long, the bracts triangular to linear or foliaceous, 1-35 mm, usually less than 5 mm long. *Flowers* 7-10 mm broad, the buds 1-3 mm in diam, the pedicels to 1-6 mm long; sepals 4, rarely 3 or 5, 2-3 mm long, 2-3 mm wide, the inner 2 medially glabrous, laterally densely stellate, ciliate, the outer 2 glabrous except the submarginally stellate border, all submarginally stellate, glabrous elsewhere within; petals 4, rarely 3 or 5, white, oblong to obovate, 4-5 mm long, 2-4 mm wide, obtuse to incised at the apex; stamens 20-30, the filaments 1.5-2.5 mm long, the anthers 1.0-1.5 mm long; ovary 4-, rarely

3- or 5-locular, globose, 4-, rarely 3- or 5-sulcate, glabrous, the styles to 1 mm long at anthesis, the stigmas simple. *Berries* to 8 mm in diam, globose, 4-, rarely 3- or 5-sulcate, glabrous.

Southern Mexico to Colombia.

CANAL ZONE: Barro Colorado Island, *Bangham 578* (A, F), *Salvoza 998* (A.) COCLÉ: El Valle de Antón, *Allen 3630* (MO, NY, US), *Seibert 429* (A, F, NY); N of El Valle, *Allen 2180* (GH, MO, US); between Las Margaritas & El Valle, *Woodson et al. 1733* (MO, NY); trail to Las Minas, N of El Valle de Antón, *Allen 2464* (F, MO, NY, US), *3706* (MO); N rim of El Valle, *Allen 1895* (GH, MO, NY, US). PANAMA: Cerro Azul, *Dwyer 2051* (MO).

One of the few American species capable of spreading across lowland barriers, *S. laevigata* is known from southern Mexico to South America. With its nearly glabrous leaves and small tetramerous flowers, it is the most easily identified of all the American Saurauias.

4. SAURAUIA SEIBERTII Standley, Ann. Missouri Bot. Gard. **26:** 290. 1939.—Fig. 5.

Tree to 25 m, sparingly pubescent. *Leaves* with the blade elliptic to obovate, the apex acute to acuminate, the base obtuse, the margins serrulate, 9-21 cm long, 3-8 cm wide, chartaceous, the secondary veins 10-18 pairs, the tertiary veins immersed, scarcely more prominent than the lesser reticulation, scattered-tufted to glabrous between the sparingly tufted to glabrous veins above, scattered-clustered between the abundantly to scattered heterotrichous veins beneath; petioles 2-4 cm long, 1-2 mm in diam, flattened to canaliculate above. *Inflorescence* 26- to 52-flowered, rarely fewer, 13-28 cm long, 6-9 cm wide, the primary peduncle 6-15 cm long, the bracts linear to triangular, 2-8 mm long, sometimes foliaceous, to 50 mm long. *Flowers* 15-22 mm broad, the buds to 6-7 mm in diam, the pedicels 5-20 mm long; sepals 5, 4-6 mm long, 3-6 mm wide, the inner 2 medially densely heterotrichous, laterally densely appressed-pubescent, the imbricate sepal densely heterotrichous on the exterior half, densely appressed-pubescent on the interior half, the outer 2 densely heterotrichous, all densely appressed-pubescent within; petals 5, white, oblong to obovate, 6-9 mm long, 3-8 mm wide, obtuse to incised at the apex; stamens 39, rarely ca 25, the filaments 2.0-2.5 mm long, the anthers 2.0-2.5 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the styles obsolete to 4 mm long, the stigmas simple to capitate. *Berries* to 8 mm in diam, globose, 5-sulcate, glabrous.

Known only from Panama.

BOCAS DEL TORO: Robalo trail, *Allen 4968* (MO). CHIRIQUÍ: along Río Caldera, *Woodson et al. 1020* (A, F, K, MO, NY, US, type); Río Chiriquí Viejo valley, *P. White 151* (MO), *G. White 110* (MO); Boquete, Palo Alto, *Stern et al. 1075* (MO, US).

Saurauia Seibertii is apparently endemic to Panama. The specimen collected by Allen in Bocas del Toro is aberrant. It lacks the many-flowered inflorescence so characteristic of the other specimens, but agrees with them in the foliar clustered and tufted trichomes, the smooth leaves, which are nearly glabrous above, and the reticulating tertiary veins.

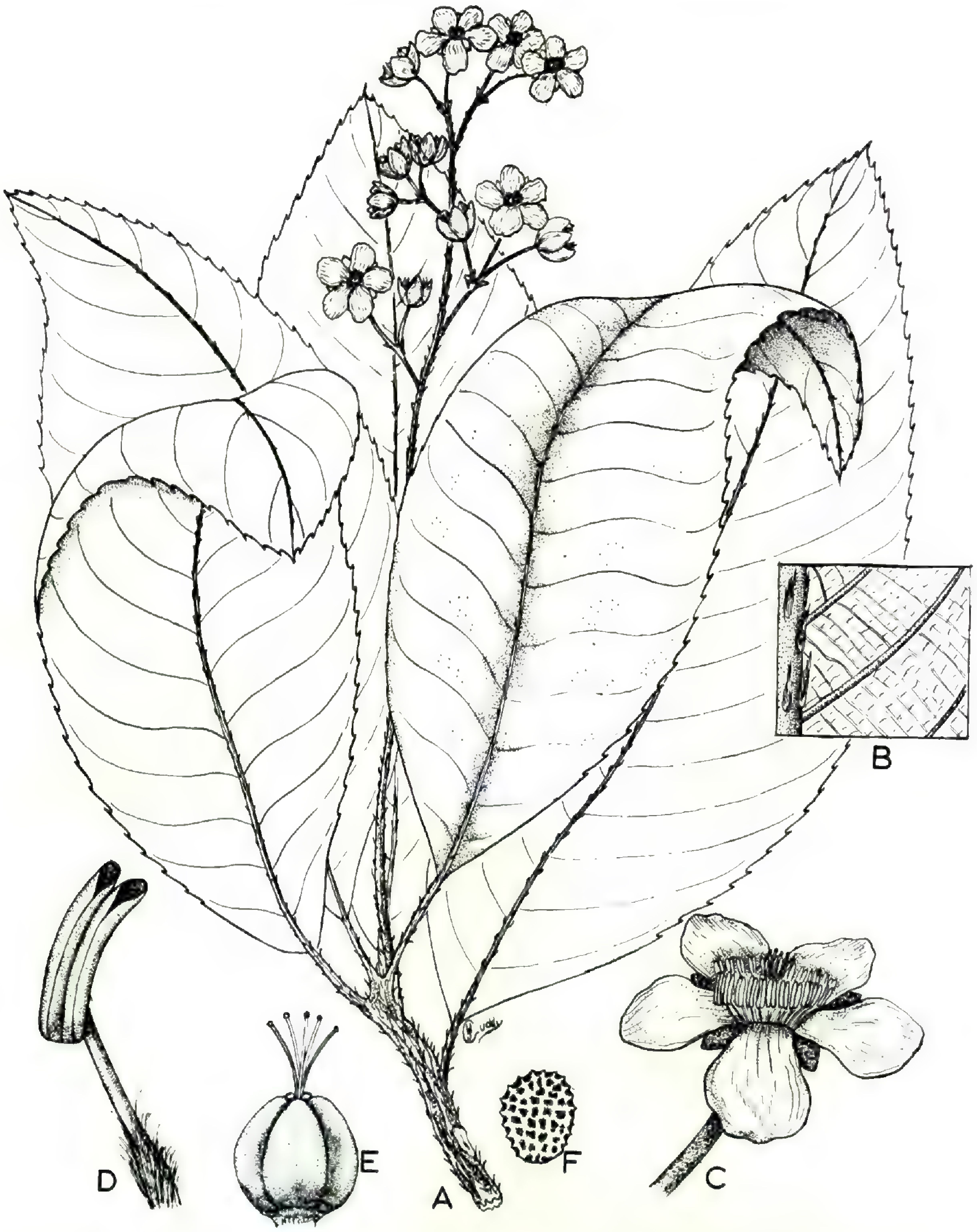

Fig. 5. Saurauia Seibertii Standley: A, flowering branch (×½); B, indumentum of lower leaf surface; C, flower (×2); D, stamen (×10); E, pistil (×5); F, seed (×10).

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